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THE AMPHIPOD SUPERFAMILY TALITROIDEA IN THE NORTHEASTERN PACIFIC REGION. I. FAMILY TALITRIDAE: SYSTEMATICS AND DISTRIBUTIONAL ECOLOGY.

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Abstract

Based on material obtained by field expeditions of the National Museums of Canada since 1955, and from other sources, this study provides new information on the distribution and ecology of semiterrestrial and terrestrial amphipods of the North American Pacific and adjacent coastal marine regions. It revises the component species within formal new generic and informal systematics-ecological groupings, based mainly on newly recognized taxonomic characters and employing numerical taxonomic methodology. The study also outlines primary factors that contribute to the anomalous regional combination of primitive and advanced morphological types within beach fleas and sandhoppers, and the total absence of native terrestrial species in the North American Pacific coast.

Herewith recorded and/or described in the region from Alaska to Baja California, are the following beach flea species: ***Traskorchestia*** new genus, and species *T. ochotensis* (Brandt), *T. traskiana* (Stimpson), and *T. georgiana* (Bousfield); ***Paciforchestia*** new genus, and species *P. klawei* (Bousfield); ***Transorchestia*** new genus, and species *T. enigmatica* (Bousfield & Carlton); and ***Platorchestia*** new genus, and ***P. chathamensis*** new species; the following sandhopper species: *Megalorchestia* Brandt, and species *M. pugettensis* (Dana), *M. corniculata* (Stout), *M. benedicti* (Shoemaker), *M. californiana* Brandt, *M. columbiana* (Bousfield), *M. minor* (Bousfield) and ***M. dexterae*** new species; and the introduced landhopper species *Arcitalitrus sylvaticus* (Haswell) and *Talitroides topitotum* (Burt). From adjacent regions, similarly treated are the sandhopper genera ***Trinorchestia*** new genus, and species *T. trinitatis* (Derzhavin) from the northwestern Pacific region; and from the Pacific coast of Mexico and Central America the sandhoppers ***Pseudorchestoidea*** new genus, with species *P. gracilis* (Bousfield & Klawe), *P. meridionalis* (Schuster), ***P. mexicana*** new species and *P. biolleyi* (Stebbing). Taxonomically pertinent descriptions and redescriptions are provided for ***Protorchestia*** new genus and species *P. nitida* (Dana), and *Transorchestia chiliensis* (Milne-Edwards) from southern Chile; *Orchestoidea tuberculata* Nicolet from central Chile; *Talitrus saltator* Latreille from the eastern Atlantic, and *Orchestia* (sens. str.) from the Atlantic-Caribbean region.

Résumé

De nouvelles données, fondées sur des spécimens recueillis lors d'expéditions du Musée national des Sciences naturelles depuis 1955 ou provenant d'autres sources, apparaissent dans cette étude sur la répartition et l'écologie des amphipodes terrestres et semi-terrestre de la côte du Pacifique en Amérique du Nord et des régions côtières adjacentes. Les espèces étudiées sont révisées et reclassées formellement dans de nouveaux genres et officieusement en groupements écosystématiques, surtout en fonction de caractères taxinomiques nouvellement reconnus et suivant une méthodologie numérique de taxinomie. L'étude décrit aussi les principaux facteurs favorisant l'anomalie que constitue la présence, dans une même région, de types morphologiquement primitifs et avancés de talitres des plages et de talitres des sables, et l'absence totale d'espèces terrestres indigènes sur la côte Pacifique de l'Amérique du Nord.

Pour la région s'étendant de l'Alaska jusqu'en Basse Californie, on signale et (ou) décrit dans l'étude les espèces suivantes de talitres des plages : nouveau genre ***Traskorchestia*** et espèces *T. ochotensis* (Brandt), *T. traskiana* (Stimpson) et *T. georgiana* (Bousfield); nouveau genre ***Paciforchestia*** et espèce *P. klawei* (Bousfield); nouveau genre ***Transorchestia*** et espèce *T. enigmatica* (Bousfield & Carlton); et nouveau genre ***Platorchestia*** et nouvelle espèce ***P. chathamensis***; les espèces suivantes de talitres des sables : genre *Megalorchestia* Brandt et espèces *M. pugettensis* (Dana), *M. corniculata* (Stout), *M. benedicti* (Shoemaker), *M. californiana* Brandt, *M. columbiana* (Bousfield), *M. minor* (Bousfield) et nouvelle espèce ***M. dexterae***; et les espèces introduites de talitres terrestres *Arcitalitrus sylvaticus* (Haswell) et *Talitroides topitotum* (Burt). Pour les régions adjacentes, on étudie de manière semblable les talitres des sables suivants : nouveau genre ***Trinorchestia*** et espèce *T. trinitatis* (Derzhavin) de la région du Pacifique nord-ouest; et nouveau genre ***Pseudorchestoidea***, avec espèces *P. gracilis* (Bousfield & Klawe), *P. meridionalis* (Schuster), ***P. mexicana*** (nouvelle espèce) et *P. biolleyi* (Stebbing), de la côte Pacifique du Mexique et de l'Amérique centrale. Font l'objet de descriptions et redescriptions taxinomiques pertinentes : nouveau genre ***Protorchestia*** et espèces *P. nitida* (Dana) et *Transorchestia chiliensis* (Milne-Edwards) du sud du Chili; *Orchestoidea tuberculata* Nicolet du centre du Chili, *Talitrus saltator* Latreille de l'est de l'Atlantique et *Orchestia* (*sensu stricto*) de la région Atlantique-Antilles.

ABBREVIATIONS FOR FIGURES

A1 .....antenna 1
A2 .....antenna 2
calc .....calceolus
Hd .....head
Pl .....pleopod
Uros .....urosome
U .....uropod
LL .....lower lip
Mx1 .....maxilla 1
Mx2 .....maxilla 2
Mxpd ....maxilliped
♂ .....male
♀ .....female
subad ....subadult

Md .....Mandible
Lft .....left
Rt .....right
UL .....upper lip
BrPl .....brood plate
BrSet ....brood setae
Ep .....epimeral plate
Gn1 .....gnathopod 1
Gn2 .....gnathopod 2
P .....peraeopod
Cx .....coxal plate
imm .....immature
juv .....juvenile
dctl .....dactyl

Introduction

The long, much-indented North American Pacific coastline is characterized by diverse rocky, sandy, and estuarine intertidal habitats. The region is washed by cool nutrient-rich ocean currents that support lush growths of attached marine algae and sea grasses, and offers ample environmental scope for members of the shore-dwelling gammaridean superfamily Talitroidea. Until very recently, however, only 23 species in six talitroidean families had been recorded in the coastal marine region from Alaska to southern California (Bousfield, 1975, 1979d; Barnard, 1975) of which 11 species were members of the semiterrestrial and terrestrial family Talitridae. Early records of North Pacific species, especially of the far-eastern seas of the USSR, had been summarized admirably by Gurjanova (1951) and Bulycheva (1957). Contributing mainly to taxonomic, distributional and ecological information on regional talitrids during the post-World War II period were the studies of Barnard (1954, 1955, 1964) and Bousfield (1957, 1958, 1961, 1970). Despite these noteworthy advances, several taxonomic problems of shore-dwelling talitrids (e.g., Bousfield, 1957; Bousfield & Klawe, 1963) remained unresolved and distributional records were spotty and incomplete. Characterization of genera and species based almost solely on characters of the gnathopods, an inheritance from 19th century taxonomists, has only recently been replaced or supplemented by more reliable and phyletically significant characters from all body regions (e.g., Bowman (1977), Friend (1980), and Bousfield (in prep.))[1]. Also, much more extensive amphipod material has been obtained in the Canadian Pacific and adjacent coastal regions since 1955 and especially since 1966 (see station lists of Bousfield and Jarrett, 1981). Recent analysis of this material has filled in many of the early distributional hiatuses and permitted more accurate comparison of the eastern and western North Pacific faunas and of the total North Pacific rim fauna (lat. 35°N–65°N) with the corresponding North Atlantic talitrid fauna (see Bousfield, 1979d, 1981). The richer and more diverse North Pacific fauna undoubtedly reflects the much greater age of its coastline and presumed more prolonged evolutionary opportunities. Despite changing configurations through accretion of microcontinents during the Palaeozoic, this coastline has remained an essentially open surf coast since the early Mesozoic (see Howarth, 1981; Ben-Abraham, 1981).

Based mainly on material obtained during field expeditions of the National Museums of Canada in the Alaska to California coastal marine regions, especially since 1966, the present study provides detailed records of the distribution and ecology of regional species of Talitridae; it furthermore attempts to group the species more realistically and formally on a systematics-ecological basis, and relates these components to faunas of adjacent and world-wide regions that have previously been described and/or are currently under revision.

[1]Bousfield, E.L. A revised classification of Talitrid amphipods (Crustacea: Amphipoda: Talitridae). (In prep.)

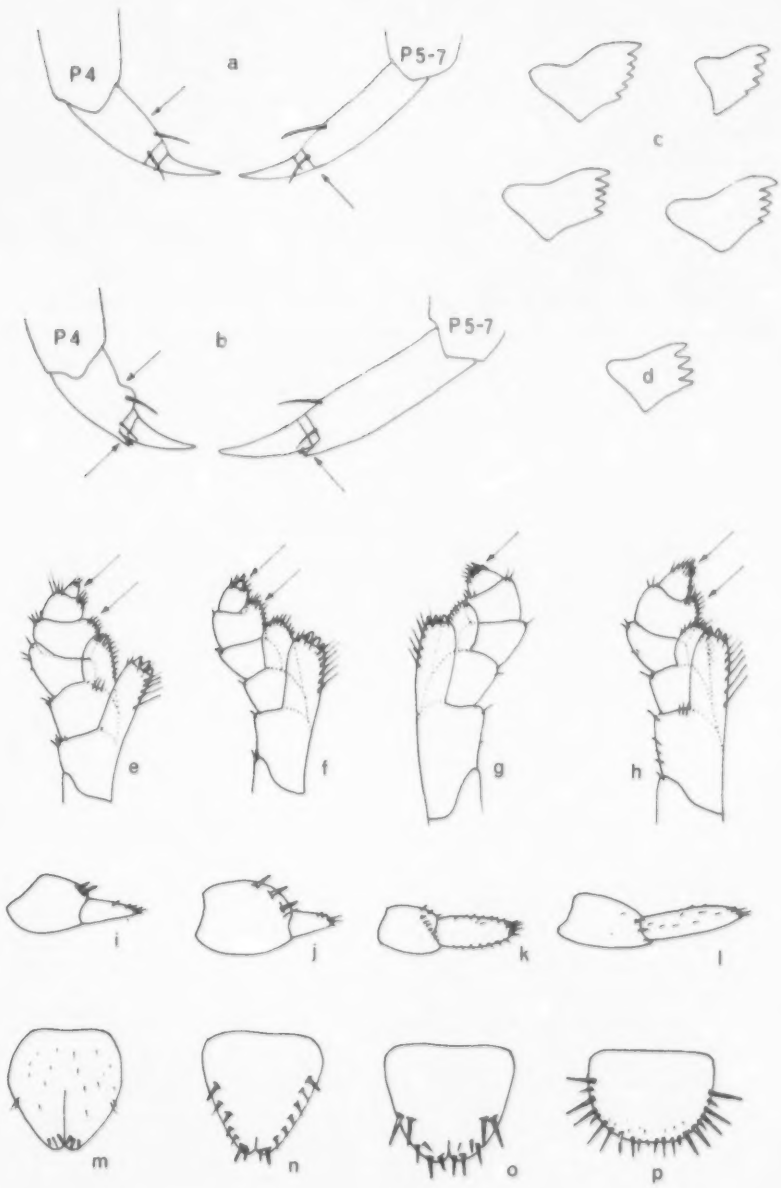

Figure 1. TALITRIDAE. Major Taxonomic Characters.
a, b: peraeopod dactyls; c, d: mandibular left lacinia mobilis; e–h: maxilliped; i–l: uropod 3; m–p: telson.

Systematics

Recent advances in talitroidean systematics (e.g., Bousfield, 1979a, 1981, in prep.[1]; Friend, 1980) have underscored the family level distinctiveness of the Talitridae and facilitated recognition of more natural (phyletic) species groupings. Newly recognized taxonomic characters especially of mouthparts, peraeopods, and surface ultrastructure (see especially Bousfield in prep.[1]; Bousfield and Halcrow, in prep.) are used herewith to supplement and clarify previous taxonomic diagnoses of the family and component genera.

Superfamily Talitroidea Bulycheva 1957, emend Bousfield 1979a
Family Talitridae Bulycheva 1957, emend Bousfield 1979a, 1982

Body smooth, rarely rugose; pleon rarely dorsally toothed; urosome short, segments 2 and 3 usually telescoping dorsally into 1; animal capable of saltation (in air). Eyes medium to very large, often nearly dorsally contiguous, rarely small or lacking. Antenna 1 very short, rarely longer than peduncle of antenna 2 which is often elongate and sexually dimorphic. Buccal mass directly beneath head or slightly prognathous. Upper lip rounding below; lower lip lacking inner lobes, varying little. Mandible, left lacinia 4 or 5-(occasionally 6-) dentate, right lacinia usually tri- or quadricuspate. Maxilla 1, palp minutely 2-segmented or lacking; maxilla 2, inner plate shorter, single stout proximal plumose seta, varying little; maxilliped plates often small and weakly armed, palp segment 4 much reduced or lacking, rarely unguiform. Coxa 1 reduced, not posteriorly cuspate; coxae 2–4 deeper, each with distinct posterior marginal cusp, which may be small or lacking. Gnathopods unlike, strongly sexually dimorphic except in some terrestrial genera and one intertidal genus; gnathopod 1 weakly subchelate or simple (lacking palm), distal segments often tumescent behind (especially in male); gnathopod 2 minutely subchelate or chelate and propod mitten-shaped in females, immatures and many terrestrial males, often powerfully subchelate and of "amplexing" form especially in semi-terrestrial males. Peraeopods slender, spinose, occasionally fossorial; dactyls cuspidactylate and unlike in peraeopods 3 and 4, or non-cuspidactylate and alike. Peraeopod 5 usually much shorter than 6 and 7, all trending to dissimilarity of form and size in advanced groups. Pleopods slender, variously modified, reduced, or vestigial, rarely sexually dimorphic. Uropods 1 and 2 well developed, rami moderately long, spinose apically and usually marginally, uropod 1 often set on short "prepeduncle"; uropod 3 uniramous. Telson lobes variously fused, usually slightly separated distally, and armed apically and often dorsally with spines. Coxal gills short, plate-like or sac-like (marine intertidal species), or large, pleated, convoluted or lobate (most terrestrial species); sternal gills lacking. Brood plates variable; usually subovate, marginally setose, setae hook-tipped in plesiomorphic species, but often very reduced, linear, with marginal setae few and simple in apomorphic species.

Recent revision of the 200+ known world species (Bousfield, in prep.)[1] has informally subdivided family members on a systematics-ecological and behavioural basis to encompass (1) palustral talitrids (semi-aquatic in salt marshes and mangrove swamps)[2], (2) beach fleas (mainly intertidal and coastal leaf-litter, non-substrate-modifying talitrids), (3) sandhoppers (intertidal substrate-modifying talitrids of sandy beaches), and (4) landhoppers (truly terrestrial, supra-tidal non-substrate-modifying talitrids). Since each group contains at least two obviously convergent generic morphotypes and is therefore polyphyletic, no formal recognition of these four groups is proposed. However, the system has some practical taxonomic application and is utilized herewith.

[1]Bousfield, E.L. A revised classification of Talitrid amphipods (Crustacea: Amphipoda: Talitridae). (In prep.)
[2]Records from Pacific coast of Central America and Galapagos include those of Stebbing (1906b) and Monod (1970) for "*Orchestia*" *costaricana*, and Bousfield (in prep.).

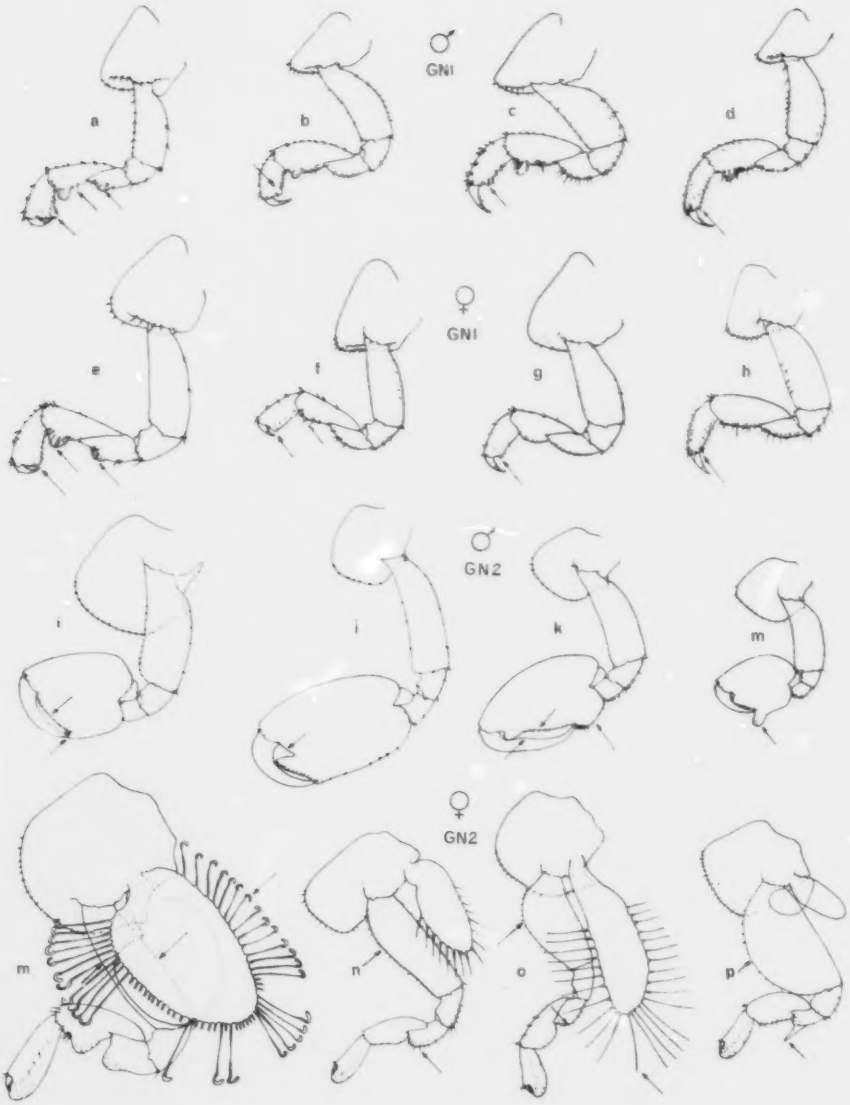

Figure 2. TALITRIDAE. Major Taxonomic Characters; Gnathopods.
a–d: gnathopod 1 ♂; e–h: gnathopod 1 ♀; i–l: gnathopod 2 ♂; m–p: gnathopod 2 ♀.

Key to principal systematics-ecological groupings of Talitridae

1. Dactyls of peraeopods 3–7 non-cuspidactylate; peraeopods 3 and 4 dactyls alike; segments 5 subequal (figs. 1a, 3h) 2
   Dactyls of peraeopods 3–7 cuspidactylate; dactyl of peraeopod 4 variously thickened and "pinched" (notched behind), unlike that of peraeopod 3; peraeopod 4, segment 5 distinctly shorter than in peraeopod 3 (figs. 1b, 3i) 4
2. Peraeopods 5–7 subsimilar in form, increasing in length posteriorly (fig. 31); coxal gills plate-like, subsimilar on peraeopods 2–6; gnathopod 1 distinctly subchelate in male and female, palm not exceeded by dactyl (figs. 2a, e) 3
   Peraeopods 5–7 more or less unequal in form and size; coxal gills various, usually convoluted and complexly lobate, unlike on peraeopods 2–6; gnathopod 1, palm weak or lacking (especially ♀), exceeded by dactyl (figs. 2g, h) ..... non-cuspidactylate landhoppers (incl. *Arcitalitrus*, p. 55)
3. Mandibular left lacinia mobilis 4-dentate (fig. 1d); semi-aquatic in salt marshes, mangrove swamps, and some fresh-waters (New Caledonia) ..... palustral talitrids (not treated hereby)
   Mandibular left lacinia mobilis 5-dentate (fig. 1c); intertidal on rocky shores ..... non-cuspidactylate beach fleas (*Protorchestia*, p. 7)
4. Appendages (antennae, gnathopod 1, peraeopods, uropods) stout, more or less strongly spinose and modified for burrowing (figs. 3g, 1); pleopod peduncles marginally spinose (figs. 3p, q, r); substrate-modifying burrowers ..... sandhoppers 5
   Appendages slender, with slender spines, not modified for burrowing (figs. 3d, n); pleopod peduncles very weakly or not marginally spinose (fig. 3o); non-substrate modifiers of rocky (rarely sandy) beaches and forest leaf litter ..... beach fleas and cuspidactylate landhoppers 6
5. Mandible, left lacinia 5- or 6-dentate; uropod 3, ramus relatively long (figs. 1k, l); gnathopod 2 (♀), basis broadened anteriorly (fig. 2p) ..... 5-dentate sandhoppers (p. 24)
   Mandible, left lacinia usually 4-dentate; uropod 3 short, ramus < peduncle (figs. li, j); gnathopod 2 (♀) basis narrow (fig. 2n) ..... 4-dentate sandhoppers (p. 24)
6. Maxilliped palp, segments 2 and 3 broadly expanded, segment 2 with medio-distal lobe and strongly spinose medial margin (figs. 1f, g); coxal gills 3–5 relatively small, smaller than 2 and 6; gnathopod 2 (♂) of functionally amplexing form, powerfully subchelate (fig. 2i); peraeopod 4 dactyl usually strongly pinched or incised posteriorly, different from peraeopod 3 (fig. 1b) ..... beach fleas ("Orchestia" groups) (p. 5)
   Maxilliped palp, segments 2 and 3 usually spinose, not broadly expanded, segment 2 never with inner distal lobe (fig. 1e); coxal gills 3–5 (as well as 2 and 6) large, convoluted or modified; gnathopod 2 (♂) usually mitten-like (as in ♀ and imm.) (fig. 2n), if subchelate, dactyl attenuated; peraeopod 3 and 4 dactyls not strongly different (fig. 3h) ..... cuspidactylate landhoppers (incl. *Talitroides topitotum*) (p. 55)

Section I. Beach Fleas (Non-substrate modifiers *sensu* MacIntyre, 1963)

Key to genera of beach fleas of the North Pacific rim region
and selected world-wide genera
(includes *Traskorchestia*, *Paciforchestia*, *Transorchestia*, *Orchestia*, *Protorchestia*, *Platorchestia*)[1]

1. Mandibular left lacinia 5-dentate; antenna 2 not, and peraeopods 6 and 7 usually not noticeably sexually dimorphic in form (except *Traskorchestia ditmari*) 2
   Mandibular left lacinia 4-dentate; antenna 2 and peraeopods 6 and 7 more or less strongly sexually dimorphic, often incrassate or thickened or of different form in ♂ (figs. 3c, k) 4
   Mandibular left lacinia 5-dentate; antennae and peraeopod 7 (often also 6) incrassate (♂) .... *Platorchestia* n.g. (p. 26)

[1]Genus *Platorchestia* is included also in the sandhoppers.

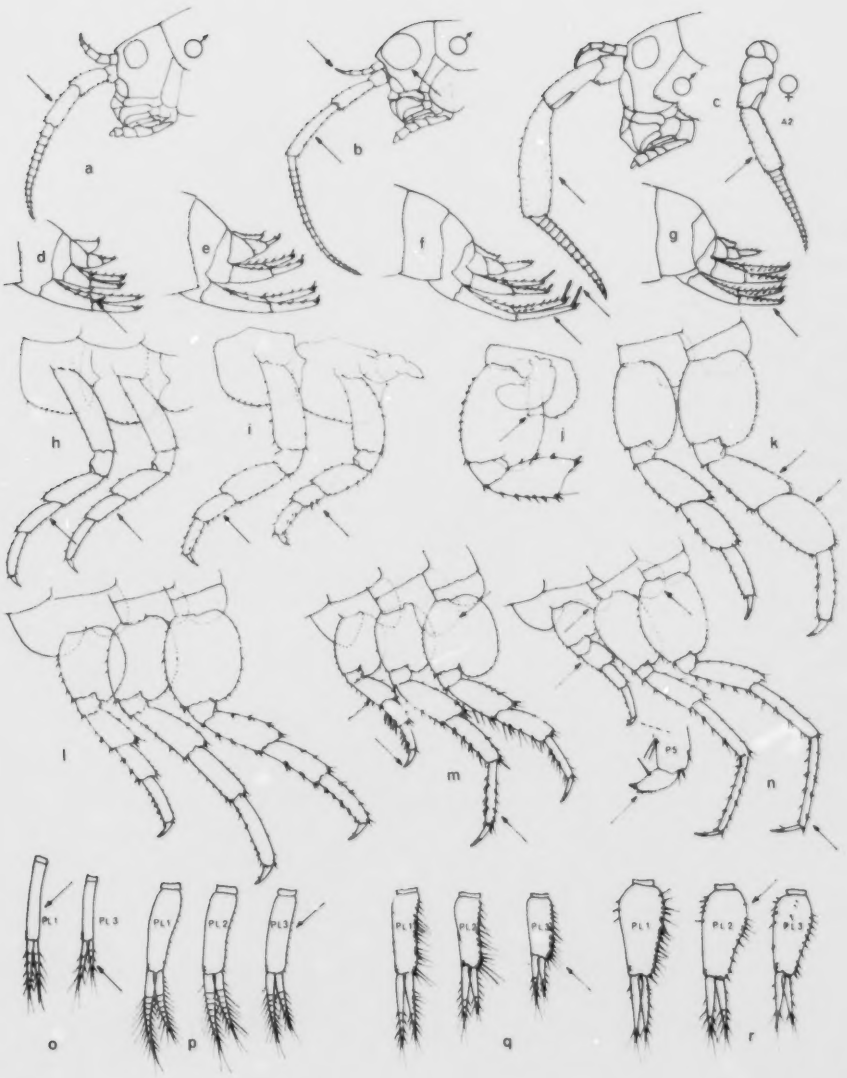

Figure 3. TALITRIDAE. Major Taxonomic Characters.
a–c: head & antennae; d–g: urosome & uropods; h, i: peraeopods 3 & 4; j, k: peraeopods 6 & 7; l–n: peraeopods 5, 6, & 7; o–r: pleopods.

2. Maxilliped palp distinctly 4-segmented (fig. 1e); gnathopod 2 (♀), basis linear, not expanded (fig. 2m); coxal gills 2–6 plate-like, subsimilar; telson lacking dorsal spines (fig. 1m) .... *Protorchestia* n.g. (Southern Hemisphere) (p. 7)
Maxilliped palp obscurely 4-segmented, 4th masked by spines of 3 (figs. 1f, g); gnathopod 2 (♂), basis more or less expanded anteriorly (fig. 2o, p); coxal gills modified, 3, 4 and 5 reduced; telson with dorsal, marginal, and apical spines (figs. 1n, o) 3

3. Uropod 1 with strong distolateral (inter-ramal) spine (fig. 3d); telson longer than broad, narrowing distally, with single dorsolateral spine (fig. 8); gnathopod 1 (♀), segments 5 and 6 posteriorly tumescent, dactyl not exceeding palm (fig. 2e); brood plate setae simple (fig. 2o) .... *Paciforchestia* n.g. (p. 17)
Uropod 1 lacking distolateral spine (fig. 3e); telson short, broader than long, with groups of dorsal and marginal spines (fig. 1o); gnathopod 1 (♀), segments 5 and 6 not tumescent posteriorly, dactyl slightly exceeding palm (fig. 2f); brood plate setae hook-tipped (fig. 2m) .... *Traskorchestia* n.g. (p. 9)

4. Gnathopod 1 (♀), dactyl barely or not exceeding distinct palm (fig. 2f); telson elongate, narrowing distally, lobes with dorsolateral row of spines (fig. 1n); brood plate setae hook-tipped .... *Transorchestia* n.g. (p. 19)
Gnathopod 1 (♀), palm short, distinctly exceeded by dactyl (fig. 2g); telson short, with dorsal, marginal, and apical groups of spines (fig. 1o); brood plate setae simple ..... *Orchestia* Leach

Protorchestia new genus

Diagnosis

Small, littoral and supralittoral talitrids characterized by *Hyale*-like, unmodified bodies; eyes dorsolateral, nearly contiguous; inferior antennal sinus very shallow; antenna 1 equal to or slightly exceeding peduncle 4 of antenna 2; antenna 2 not elongate nor sexually dimorphic in form. Buccal mass not prognathous; mandibular left lacinia 5-dentate, right lacinia quadricuspate (?); maxilliped palp distinctly 4-segmented, 4th not unguiform, segment 2 expanded medially but lacking inner distal lobe. Coxae 2–4 rounded below, hind margin with cusp. Gnathopod 1 (both sexes) fully subchelate (stronger in ♂), dactyl not exceeding (usually shorter than) palm, segments 4, 5 and 6 tumescent posteriorly; gnathopod 2 (♂) powerfully subchelate, propod short, deep, palm smoothly convex; gnathopod 2 (♀) basis linear, not expanded, segment 3 short, segments 4 and 5 tumescent behind, 6 short, mitten-shaped. Peraeopods 3–7 non cuspidactylate, unguis short; peraeopods 3 and 4, all segments closely subsimilar, segments 5 subequal; peraeopods 5–7 similar in form (homopodous), increasing in length posteriorly, bases rounded behind, segment 5 not short, peraeopod 7 not incrassate in ♂; coxa 5 aequi- or slightly anterolobate; coxa 6, hind lobe steeply oblique. Abdominal side plates 1–3 nearly smooth behind, hind corners subacute; pleopods normal, linear, peduncles each with 2 retinacula, margins not spinulose. Uropods 1 and 2 short, outer ramus smooth, peduncle with distolateral (inter-ramal) spine; uropod 3 short, ramus tapering, with apical and marginal spines. Telson lobes narrowing and separated distally, with apical spines only. Coxal gills plate-like, subsimilar. Brood plates (♀) large, subovate, smallest on peraeopod 5, marginal setae long, numerous, hook-tipped.

Type-species: *Orchestia nitida* Dana 1852 (Cape Horn region, South America)

Additional species:

Protorchestia campbelliana (Bousfield 1964) (Campbell Island, New Zealand)

Parorchestia americana Bousfield 1964 (*nomen nudum*) Uruguay.

Etymology

The generic name signifies its very primitive morphology, embodying exclusively plesiomorphic characters, that is probably close to the first or ancestral talitrid morphotype. Gender: Feminine.

Remarks

The following species could be included in this genus except that the left mandibular lacinia is 4-dentate (a presumed apomorphic condition), antenna 1 nearly equals the peduncle of antenna 2, uropod 3 ramus lacks marginal spines, and peraeopod dactyls are more elongate, among other differences: *Parorchestia rectipalma* K.H. Barnard 1940 (South Africa), and a series of undescribed estuarine species from Tasmania

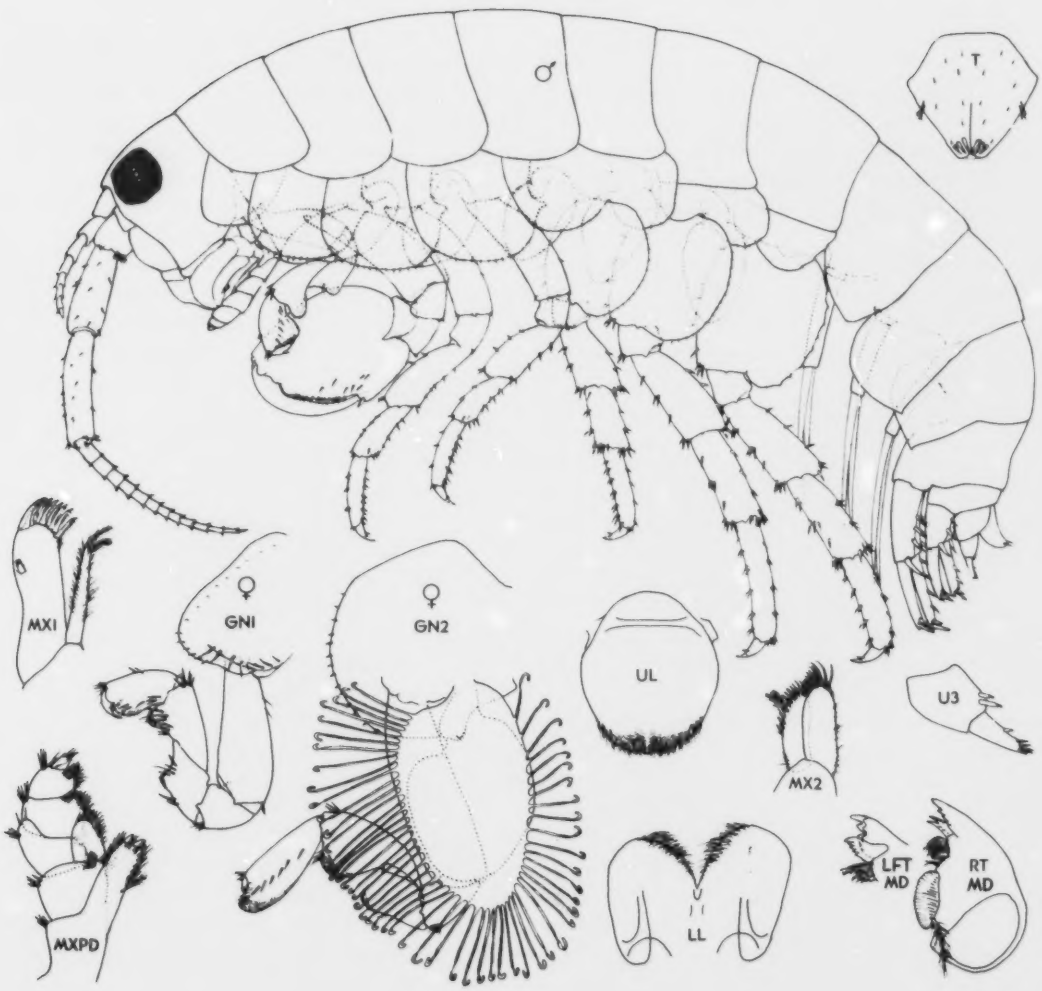

Figure 4. *Protorchestia nitida* (Dana). Puerto Robalo, Chile. ♂ - 10.5 mm; ♀ ov. - 6.5 mm.

and New Zealand (Bousfield, unpublished information). Remarkably, *Protorchestia* is plesiomorphic in all characters considered in this study (Tables II, IV, figs. 26, 28) and little advanced beyond its presumed aquatic hyalid ancestors.

Protorchestia nitida (Dana 1852)
Figure 4

Orchestia nitida Dana 1852, p. 204; 1853, p. 868, t. 58, fig. 5a-f
:Stebbing, 1906a, p. 539

Material examined
Stn. F.1, Puerto Robalo, Isla Navarino, Chile, MW-LHW levels, 29 January, 1970, E.L. Bousfield and J.W. Markham colls., 1 ♂, 1 ♀ (ov.) (slide mounts); approximately 54 ♂♂, 38 ♀♀ (many ov.), and 80 juv. identified from 12 other stations in the Cape Horn region, Chile, February 1970. Hudson 70 Expedition, E.L. Bousfield and J.W. Markham colls., NMNS collections.

Distributional ecology
Known only from southern Chile and the Cape Horn region, mainly under algae and stones, occasionally in tide pools, from MW to lower HW levels (rarely under drift debris at HW level), and below main zone of *Transorchestia chiliensis*, mainly on protected and semi-protected beaches, occasionally in brackish water. Females ovigerous in summer (January–February), presumably annual.

Remarks
The female is very similar to *P. campbelliana* (Bousfield) but differs in the larger eye, longer telson, more elongate uropod 3, and smaller size at maturity. Although the differences are slight, species distinction is maintained pending description of the male of *P. campbelliana.*

Traskorchestia new genus

Diagnosis
Small to medium-large beach fleas characterized by: smooth, unmodified bodies; eyes lateral, not dorsally contiguous; antenna 1 equal to or slightly exceeding peduncle 4 of antenna 2, peduncle 3 longest; antenna 2 not elongate, peduncle not incrassate in male; inferior antennal sinus distinct, medium deep; buccal mass directly beneath head, not significantly prognathous; mandible, left lacinia 4 ½ (-5) -dentate, right lacinia tricuspate; maxilliped palp medium, obscurely 4-segmented (4th minute, masked by spines of 3), segment 2 broadly expanded medially, with distinct mediodistal lobe. Coxa 1 medium, half-overlapped by 2; coxae 2–4 broader than deep, lower margins nearly straight, hind margins cuspate. Gnathopod 1 (♂), dactyl shorter than palm, segments 5 and 6 (occasionally 4) tumescent behind; gnathopod 1 (♀), palm short, slightly exceeded by dactyl, segment 4, 5 not, 6 slightly posterodistally tumescent behind; gnathopod 2 (♂) powerfully subchelate, propod short, deep, palm smoothly convex; gnathopod 2 (♀), basis moderately expanded anteriorly, segment 3 short, segments 5 and 6 shallow-tumescent posteriorly. Peraeopods 3–7 cuspidactylate, dactyls (especially unguis) short; peraeopod 4, segment 5 distinctly shorter, and dactyl strongly pinched, differing from respective segments of peraeopod 3; peraeopods 5–7 more or less homopodous, increasing in length posteriorly, bases rounded behind, that of peraeopod 7 may be sexually dimorphic (e.g., *T. ditmari*); coxa 5 aequi- or slightly antero-lobate, coxa 6 hind lobe steeply oblique, anterodistally rounding. Abdominal side plates medium deep, hind corners subacute, posterior margins weakly spinulose; pleopods slender, rami normal or variously reduced, peduncles with 2 retinacula, all peduncles with a few outer marginal spines. Uropods 1 and 2 short to medium, outer ramus marginally spinose, inner ramus both margins spinose, peduncles lacking laterodistal (inter-ramal) spine; uropod 3, peduncle deep, posterior margin spinose, ramus tapering, margins and apex short-spinose. Telson short to medium, with apical and dorsal groups of spines, apex notched. Coxal gills lobate, 3–5 much smaller than 2 and 6. Brood plates (♀) large, subovate, margins with numerous long hook-tipped setae.

Type-species: *Orchestia traskiana* Stimpson 1857 (present selection)

Additional species: *Traskorchestia ochotensis* (Brandt 1851)

Traskorchestia ditmari (Derzhavin 1923)

Traskorchestia georgiana (Bousfield 1958)

Etymology
A combining form of the generic name *Orchestia* and the species name *traskiana*. Gender: Feminine.

Remarks
The genus *Traskorchestia* is closest to the austral and south Pacific new genus *Transorchestia* (Tables II, IV, figs. 26, 28), especially in the elongate segment 3 of antenna 1; relatively deep inferior antennal sinus; obscurely 4-segmented maxilliped palp; deep subchelate and distally tumescent segments of gnathopod 1 (♂); moderately expanded basis of gnathopod 2 (♀); large brood plates with curl-tipped marginal setae; short peraeopod dactyls; short, spinose uropods lacking pronounced distolateral (inter-ramal) spine; and deep, posteriorly spinose peduncle of uropod 3. *Traskorchestia* is more plesiomorphic than *Transorchestia* in the essentially 5-dentate condition of the mandibular left lacinia; non-incrassate antenna 2 (♂); smooth-palmed propod and non-sinuous dactyl of gnathopod 2 (♂); weakly (or not) incrassate condition of peraeopods 6 and 7 (♂); and oblique, rounded hind lobe of coxa 6; but is more apomorphic in the more reduced palm of gnathopod 1 (♀) with overlapping dactyl; reduced rami

and more strongly spinose peduncles of the pleopods; more heavily spinose uropods; and shorter, broader, more dorsally spinose telson. *Traskorchestia* is also more apomorphic than *Paciforchestia* in nearly all generic characters, except in the form of the brood plates and marginal setae. On the other hand *Traskorchestia* is generally more plesiomorphic than *Platorchestia*, except in the reduced dentition of the mandibular left lacinia, and the more strongly spinose rami of uropod 1, but is not more apomorphic than *Orchestia* in any character, except the more spinose pleopods.

Key to species of *Traskorchestia*

1. Peraeopod 7 (♂), posterior margin of basis straight, or basis distally widening; segment 6 distally with longitudinal facial row of brush setae; telson with 3–4 dorsolateral spine groups 2
   Peraeopod 7 (♂), posterior margin of basis evenly rounded, basis narrowing distally; segment 6 with 5–6 transverse apical brush setae only; telson lobes each with 1–2 dorsolateral spine groups 3
2. Peraeopod 7 markedly sexually dimorphic in form, basis (♂) strongly expanding postero-distally, margin deeply serrate; gnathopod 2 (♂), propod distinctly widening distally; uropod 3, peduncle with (4) 5 postero-distal spines ..... *T. ditmari* (Derzhavin)
   Peraeopod 7 slightly sexually dimorphic, basis (♂) not expanding distally, margin weakly serrate; gnathopod 2 (♂), propod margins subparallel, not distinctly widening distally; uropod 3, peduncle 3-(4) spinose ..... *T. ochotensis* (Brandt) (p. 15)
3. Antenna 1 very short, flagellum 3–4 segmented, shorter than peduncle; peraeopod 4, segment 5 very short and stout, about ½ length of segment 6; gnathopod 1 (♂), segment 4 lacking posterior "blister"; uropod 1 sexually dimorphic, outer ramus (♂) with 5–6 close-set marginal comb-spines (fig. 6) ..... *T. georgiana* (Bousfield) (p. 13)
   Antenna 1 normal, flagellum 5–7 segmented, longer than peduncle; peraeopod 4, segment 5 about ¾ length of segment 6; gnathopod 1 (♂), segment 4 with posterior "blister" (fig. 5); uropod 1 not sexually dimorphic, outer ramus (♂) with 3–4 (5) broadly spaced spines ..... *T. traskiana* (Stimpson) (p. 10)

Traskorchestia traskiana (Stimpson 1857)
Figure 5

Orchestia traskiana Stimpson 1857a, p. 90
:Stebbing, 1906a, p. 534
:Bousfield, 1958, p. 885, fig. 10d; 1975, p. 363, fig. 236; 1961, p. 3, fig. 1, 2; 1981, p. 83, fig. 17
Orchestia sp.: O'Clair, 1977, p. 446
non *Orchestia taskiana*: Bulycheva, 1957, p. 166, fig. 60

Material examined

Alaska: Amchitka, Aleutian Islands; C.E. O'Clair Plot 5, upper 1A2, 22 May 1974, 1 ♀ imm., *ibid.*, Plot 9, 1A2, 27 August 1974, 2 imm., *ibid.* (no data), 2 ♀♀, br. II.

Southeastern Alaska: 865 specimens from Bousfield & McAllister 1961 stns. (Seward to Dixon Entrance) A1, A4, A7, A8, A14, A18, A22, A25, A29, A31, A37, A38, A55, A57, A68, A75, A87, A88, A118, A121, A131, A140, A151, A159, A162, A166, A175; Bousfield 1980 stns. (Sitka region) S2, S5, S7, S11.

British Columbia: Queen Charlotte Islands; 200 specimens from Bousfield 1957 stns. H2a, H8a, H13, W2, W4a, W16, E5, E13, E14a, E17, E20, E24, E25; north mainland coast; 120 specimens from Bousfield 1964 stns. H2, H4, H9, H11, H20, H23, H34, H38, H40, H41, H42, H44, H45, H47, H51, H60, H61; central mainland coast; 40 specimens from Bousfield 1959 stns. N3, N4, N6, N11, N15, N21, N22; Vancouver Island, north outer coast, 35 specimens from Bousfield 1959 stns. O1, O2a, O3, O4, O16, and 12 specimens from Bousfield 1975 stns. P23a and P32; inner coast and Johnstone Strait, 470+ specimens from Bousfield 1959 stns. V4a, V14, V19, V20, V21, V22, V25, V26; Strait of Georgia: re-examination of Bousfield 1955 material from G4, G9, G13, G21, M1, M8, M11; Vancouver Island south end and outer coast: 100 specimens from Bousfield 1970 stns. 706, 712, 716, 719; Barkley Sound region, 70 specimens from Bousfield 1975 stns. P5, P6, P16a, P17b, P19b; 28 specimens from Bousfield 1976 stns. B3, B14; 23 specimens from Bousfield 1977 stns. B4a, B12a, B6a.

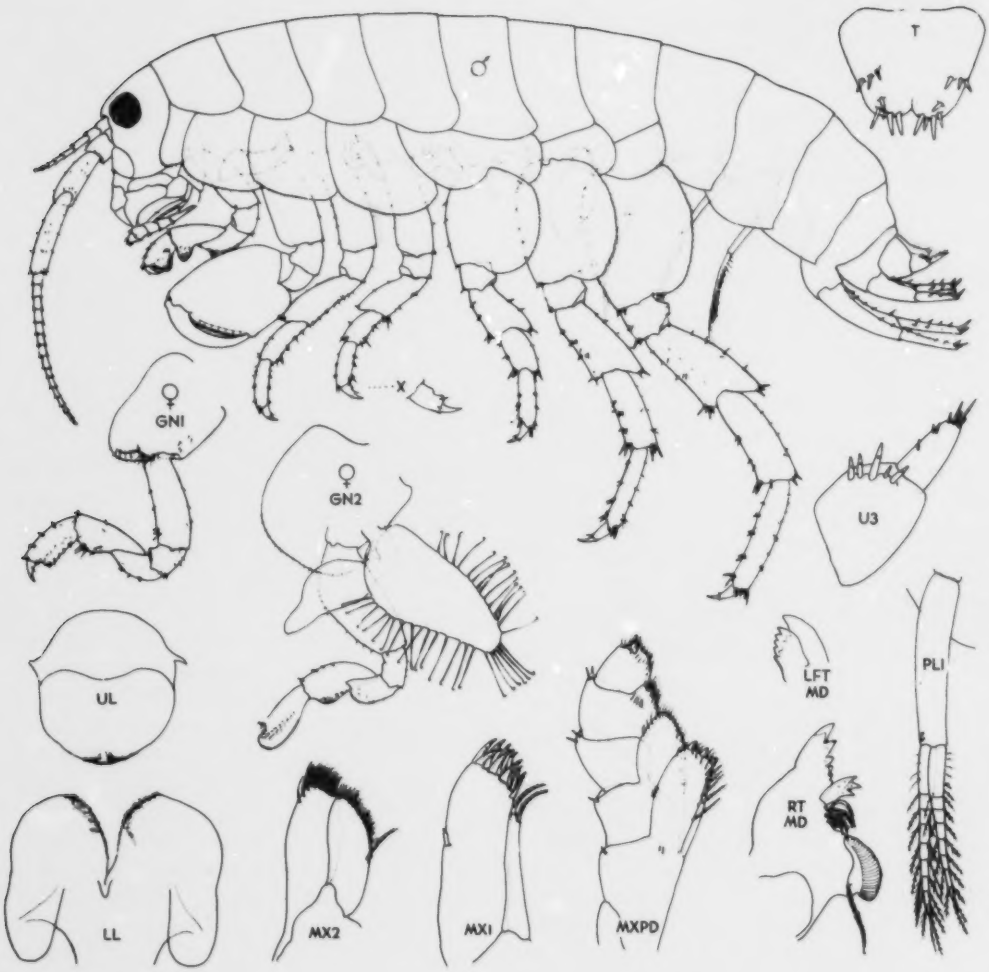

Figure 5. *Traskorchestia traskiana* (Stimpson). Piper's Lagoon, Vancouver Island, B.C. ♂ - 17.0 mm, ♀ ov. - 13.0 mm.

British Columbia: Miscellaneous collections: J.F.L. Carl, Victoria region, 1956: Ross Bay, 2 February, 6 ♂♂, 5 ♀♀ br. II, NMNS No. 5220; *ibid.*, 18 February, 5 ♂♂, 1 ♀ ov., NMNS No. 5219; Shoal Bay, 19 February, 2 ♂♂, 2 ♀♀, NMNS No. 5223; Willows Beach, 25 February, 1 ♂, NMNS No. 5217; Gonzales Bay, 27 February, 6 ♂♂ (to 19.0 mm), 1 ♀ ov., NMNS No. 5222; Cadboro Bay, 8 June, 2 ♂♂, 2 ♀♀ ov., NMNS No. 5116; *ibid.*, 15 September, 4 ♂♂, NMNS collections; *ibid.*, 1959: China Beach, 4 July, 4 ♂♂, 1 ♀, 1 imm., NMNS 5877; *ibid.*, Chatham Island, 12 July, 4 ♂♂, 1 ♀, NMNS No. 5869. C.G. Carl coll.: Pt. Grey, south entrance point to Burrard Inlet, Lot. No. 55, 10 August 1933, 39 ♂♂, 10 ♀♀ ov., NMNS collections; Savary Island, Lot No. 47, 30 March 1929, 10 ♂♂, 5 ♀♀ ov., NMNS collections; Anthony Island, Queen Charlotte Islands, 17 October 1956, 14 ♂♂, 9 ♀♀ (2 ov.), 1 imm., NMNS No. 5886; Grassy Island, B.C., 29 June 1958, 19 ♂♂, 1 ♀ ov., NMNS No. 5873; Hohuae Island, B.C., 2 July 1958, 2 ♂♂, 2 ♀♀ ov., NMNS No. 5879. S. Nash coll.: Nanoose Bay, 11 January 1979, Lot No. 1, 16 large ♂♂ (to 15.0 mm), 5 small ♂♂ (to 7.0 mm), 4 ♀♀, 9 imm.; *ibid.*, Lot No. 2,

2 ♂♂, 1 ♀ br. I; NMNS collections; R.M. O'Clair coll.: stn. 760060, Muchalat Inlet, Vancouver Island, opposite Gold River, July 1976, 2 ♂♂, 2 ♀♀ ov., NMNS collection.

Washington State: 152 specimens from Bousfield 1966 stns. W2, W4, W6, W8, W9, W11, W20, W21, W22, W26, W28, W29, W34, W35, W36, W47, W48.

Oregon coast: 38 specimens from Bousfield 1966 stns. W51, W52, W53, W55, W56, W57, W58.

California: Santa Barbara, beach intertidal, 25 October 1965, W.L. Klawe coll., 3 ♂♂, 1 ♂ transf. (at 10.0 mm), NMNS No. 13992; *ibid.*, 18 August 1969, A. Wenner coll., 9 ♂♂ (to 18.0 mm), 4 ♀♀, NMNS No. 13993; *ibid.*, 29 May 1970, 8 ♂♂, 1 ♀ ov., NMNS No. 13968. Re-examination of all material from central California published by Bousfield (1961).

Mexico: La Mission, Baja California, March 1952, T.E. Bowman coll., 3 ♂♂, USNM No. 102423; Turtle Bay, B.C., 7 June 1956, W.L. Klawe coll., 13 large ♂♂ (to 18.0 mm), 2 small ♂♂, 4 small ♀♀ ov., (to 10.0 mm), NMNS collections; El Socorro Beach, near El Rosario, HW sand, June 1980, R. Appy coll., 31 ♂♂ (to 17.0 mm), 21 ♀♀, several ov., NMNS collections. Re-examined all material from Bahia San Quintin, in Barnard (1964).

Diagnosis

Male (14–18 mm). Medium large, plesiomorphic species characterized by: antenna 1, flagellum 5–6 segmented; antenna 2, flagellum about 15-segmented, distinctly longer than unmodified peduncle. Mouthparts normal; mandible, left lacinia $4^1/_2$-dentate; maxilliped outer plate relatively tall, apex subacute. Gnathopod 1, segment 4 with small but distinct posterior blister or tumescent lobe. Gnathopod 2, propod longer than deep, palm smooth, oblique. Coxa 3, lower margin nearly straight, deepest posteriorly. Peraeopod 4, segment 5 not markedly short or thick. Peraeopods 5–7, dactyls short; bases smoothly rounding behind, margins with numerous evenly spaced basally "beaded" small spines. Peraeopod 7, segment 6 with transverse apical row of 5–6 fine setae, lacking distal longitudinal facial row of brush setae. Abdominal side plates 2 and 3, hind corners weakly produced. Pleopods normal, little reduced, rami 7–12 segmented. Uropod 1, peduncular margins with 3–5 short spines; inner ramus with 3–4 inner marginal and one or two outer marginal spines, outer ramus with 3–4 (occasionally 5 or 6) spaced outer marginal spines; uropod 2, peduncle with 3 stout inner and outer marginal spines, inner ramus with 2 inner and outer marginal spines, outer ramus with 2 short outer marginal spines. Uropod 3, peduncle with 5 posterodistal spines; ramus shorter, tapering, with 2 groups of posterior marginal spinules and slender apical spines. Telson lobes each with transverse row of mediodorsal spines, a single subapical dorsal spine and 3–4 apical spines. Coxal gill on peraeopod 6 large, about twice length of gill on peraeopod 5.

Female (13 mm ov.). Gnathopod 1, segment 6 with small posterodistal tumescence overlapped by part of unguis only. Gnathopod 2, basis widest proximally, segment 4 broadly and shallowly tumescent. Brood plate broadest proximally. Brood plate (P5) about half length of that of peraeopod 2, margins with 16–18 curl-tipped setae.

Remarks

T. traskiana bears several characters in common with *T. ochotensis*, especially in uropods, gnathopods, and overall size range; however, the lack of sexually dimorphic peraeopod 7, unreduced pleopods, and less strongly dorsally spinose telson, relate it more closely to *T. georgiana*, the other North American species. "*Orchestia*" *solifuga* Iwasa 1939 appears distinct from *T. traskiana* in the more elongate peduncular segment 3 of antenna 1, 4-dentate mandibular left lacinia, weakly lobate maxilliped palp segment 2, short palm of gnathopod 1 (♀), narrow basis of gnathopod 2 (♀), unlike sparsely crenulate basis of peraeopods 5–7, marginally setose pleopod peduncles, and sublinear uropod 3 peduncle. Until the condition of the peraeopod dactyls, coxal gills, maxilliped palp, and brood plate setae can be determined, the generic status of *O. solifuga* is uncertain.

Distributional ecology

A widely eurytopic species, occurring mainly under drift debris of rocky and stony beaches, but also on sand (co-occurring with *Megalorchestia* spp.) and in estuaries and salt marshes (often with *Paciforchestia* and *T. georgiana*) of both exposed and protected coasts, from the Aleutians and western Alaska (northern and western limits

not determined) south to northern Baja California; some populations terrestrial (sympatric with *Porcellio*) in leaf litter near shore in the Santa Barbara region. Females ovigerous during spring and summer; bearing one brood per year in the north, and in the south (south of Pt. Conception) two generations per year, with the spring brood maturing and breeding during the late summer and early fall (Wenner, 1974). Mature males of two size classes occur in warm-water shores (southern California and Strait of Georgia, B.C.).

Beach fleas and sandfleas were found by Murie (1959) and Sheffer (1959) to be the most commonly available food item of blue foxes (*Alopex lagopus* (L.)) on 22 islands of the western Aleutians, from the Near Islands (including Attu), through the Rat Islands (including Amchitka and Kiska), eastward to the Andreanof Islands (including Adak). Murie's statements that ". . . (beach fleas) swarm on the beaches where winnows of dead kelp furnish a favourable habitat. They lurk under bits of wood or anything else that may lie on the sand and preserve the required moist shelter underneath.", imply the presence of both beach fleas and sandhoppers. Scheffer (1959) specifies in his records, *Traskorchestia traskiana*, the only species identified with certainty in material of Talitridae from this region (above). Murie's further statements that "it is easy for a fox to pick up a full meal of sand fleas", and, "an island with extensive beaches, sand or gravel, is favourable for foxes", could reasonably apply to the occurrence of *Megalorchestia* spp., or even to *Trinorchestia*. Moreover, his description (p. 290) of "sand fleas" from Unimak Island (Fox Islands, eastern Aleutians) as food of red foxes (*Vulpes vulpes* L.) almost certainly would include *T. traskiana*, the dominant species in preserved material from southern Alaska.

Traskorchestia georgiana (Bousfield 1958)
Figure 6

Orchestia georgiana Bousfield 1958, p. 887, fig. 3; 1961, p. 3; 1975, p. 363; 1981, fig. 17
: Staude *et al.*, 1977, p. 12, couplet 21b and figs.

Material examined
British Columbia: Queen Charlotte Islands, Bousfield stn. E25, 8 August 1957, north end Hotspring Is., Moresby Is., 1 ♂, 1 ♀ ov., NMC-C-1981-476. Southern Mainland; E.L. Bousfield stn. EB 10, Stearman Beach, West Vancouver, 19 June 1976, 1 imm. ♀ NMC-C-1981-483. Vancouver Island. E.L. Bousfield stns. V25, V27, Little Tribune Bay, Hornby Is., drift debris under *Sargassum*, sand beach, pan traps, 30–31 July 1959, 700+ specimens (♂♂, ♀♀, imm.), NMC-C-1981-490. Savory Island, 30 March 1929, G.C. Carl coll., 1 ♀ subad., NMC-C-1981-482. Sydney, B.C. gravel beach at HW, June 1976, R. Long coll., 1 ♂ subad., 18 ♀♀ br. I & II, NMC-C-1981-487; Brady's Beach, near Bamfield, B.C., tide pools at HW, 29 July 1976, E.L. Bousfield coll., 7 ♂♂ (to 13.5 mm), 3 ♀♀ ov., 1 imm., NMC-C-1981-484. **Washington:** E.L. Bousfield stn. M10b, Boundary Bay, *Salicornia* flats, 2 September 1957, 1 ♂, NMC-C-1981-477.
California: Re-examined material from San Diego region published by Bousfield (1961).
Mexico: Turtle Bay, near Ensenada, Baja California, HW drift, 7 June 1956, W.L. Klawe coll., 14 ♂♂ (to 15.0 mm), 1 ♂ transf., 5 ♀♀ ov. (to 9.0 mm), 5 imm., NMNS Cat. No. 5123, slide mount.

Diagnosis
Male (12–14 mm). Small to medium-sized apomorphic species characterized by: antenna 1 short, flagellum 3–4 segmented; antenna 2 short, flagellum barely longer than peduncle, 12–14 segmented; maxilliped outer plate small, apex rounded, barely exceeding inner plate; coxa 2 large, rounded below, nearly masking coxa 1; gnathopod 1, segment 4 lacking posterior blister, dactyl shorter than palm; gnathopod 2, propod relatively short and deep, palm short, gently convex, nearly vertical. Peraeopod 4, segment 5 very short and thick (relative to peraeopod 3); dactyl short, strongly pinched, unguis short. Peraeopods 5–7 relatively short and small (for body), bases less broadly expanded than in *T. traskiana*, marginal spinules fewer and more widely spaced, peraeopod 7 not sexually dimorphic, hind lobe of basis distally obtuse, not evenly rounded, segment 6 with transverse apical row of 4–5 setae. Abdominal side plates 2 and 3 deep, distally broad, hind corners acute; pleopods slender, somewhat reduced, 1st slightly the shorter, rami 5–6 segmented. Uropod 1, peduncle with 8 inner and outer marginal spines, inner ramus with 4–6 inner and outer marginal spines; outer ramus with 5–6 tightly spaced outer

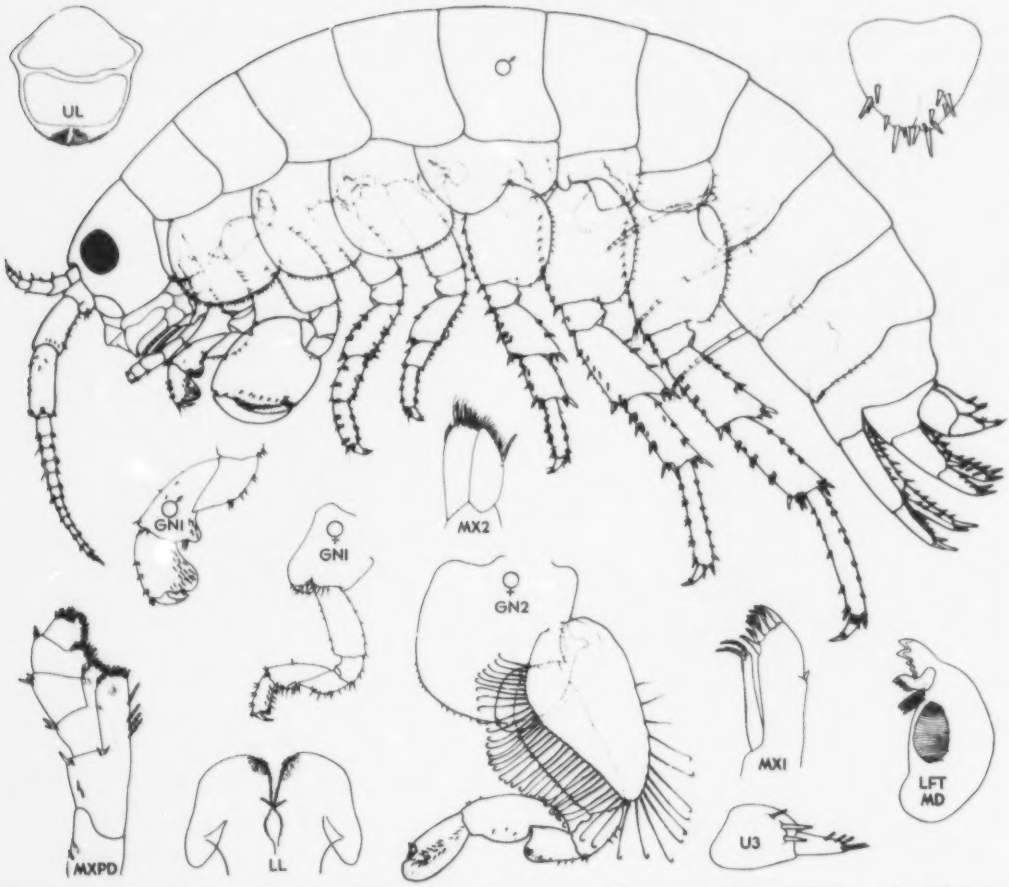

Figure 6. *Traskorchestia georgiana* (Bousfield). Cape Lazo, Vancouver Island, B.C. ♂ - 13.5 mm, ♀ - 10.5 mm.

marginal "comb-spines" (distally); uropod 2 peduncle with 4 outer marginal spines, strongest distally, inner ramus with 2–3 inner and outer marginal spines, outer ramus with 2–3 outer marginal spines. Uropod 3, peduncle short, deep, with 3 posterodistal spines; ramus short, tapering, with distal and apical short spines. Telson short, lobes each with dorsolateral medial groups of 3 spines, a subapical single spine, and 2–3 unequal apical spines. Coxal gills largest on peraeopod 2 and peraeopod 6, gill of peraeopod 6 about twice length of gill on peraeopod 5.

Female (5–8 mm). Much smaller than male at maturity. Gnathopod 1, propod slender, palm short, exceeded fully by unguis of dactyl, posterodistal angle not (or very slightly) tumescent. Gnathopod 2, basis slightly expanded proximally, margins nearly parallel, segment 4 broadly tumescent behind, 5 shallow, 6 short; brood plate narrowing distally, with about 40 long hook-tipped setae, mostly along anterior margin. Uropod 1, outer ramus with 2–3 well spaced marginal spines. Brood plate of peraeopod 5 smaller, margin with about 20 setae.

Remarks

Although related to *T. traskiana* more closely than to western Pacific species, *T. georgiana* is unique in possessing sexually dimorphic uropod 1, short pleopod 1, and females that are often barely ½ the length of males at maturity.

Distributional ecology

Occurs mainly at the drift line of protected stony and pebbly beaches, occurring on sand with windrows of eelgrass and *Sargassum*, usually

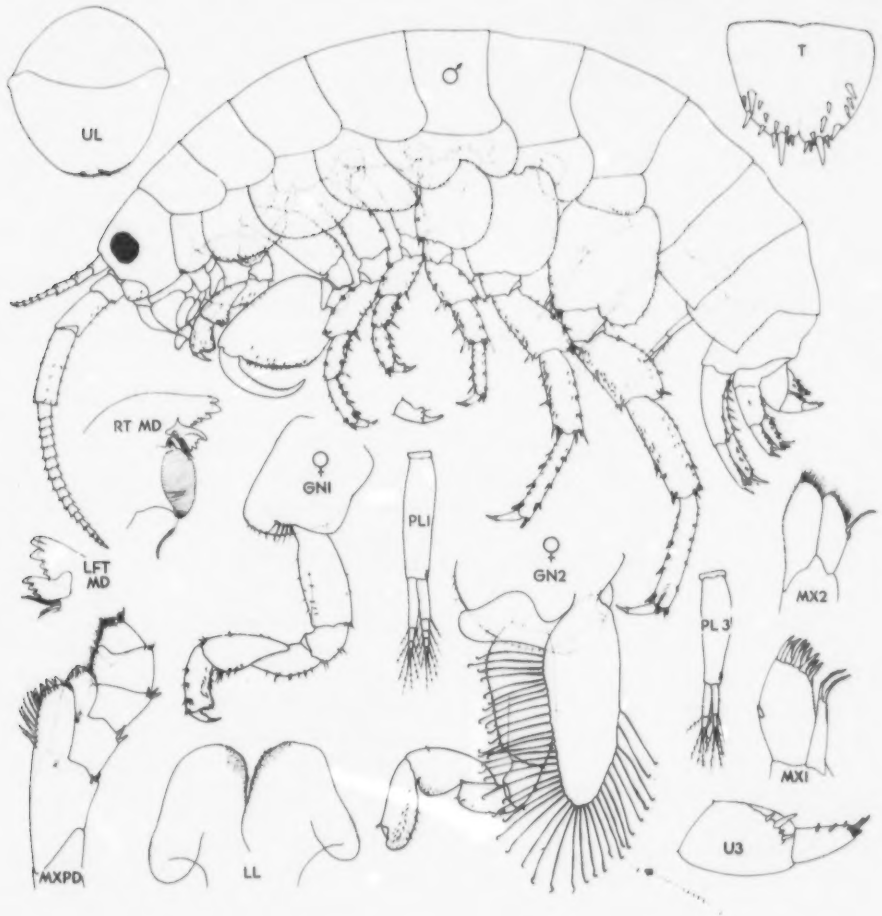

Figure 7. *Traskorchestia ochotensis* (Brandt). Orca Island, Alaska. ♂ - 15.0 mm. St. Paul Island, Bering Sea. ♀ ov. - 14.0 mm.

co-occurring with *T. traskiana*, in summer-warm bays and lagoons and inland seas, occsionally in warm tidal pools and warm springs near shore, from southern Queen Charlotte Islands and Strait of Georgia, sporadically south to Pt. Conception, and commonly southward to Baja California. Animals are slower moving, less saltatory than *T. traskiana*. Females ovigerous in spring and summer, probably with two or more generations per year in the south.

Traskorchestia ochotensis (Brandt 1851)
Figure 7

Orchestia ochotensis Brandt 1851c, p. 94, t. 6, fig. 18–26
:Stebbing, 1906a, p. 543
:Derzhavin, 1937, p. 88, pl. 1,(2)
:Gurjanova, 1951, p. 804, fig. 559
:Bulycheva, 1957, p. 166, figs. 61a, b
:Bousfield, 1981, p. 86, fig. 17
non *Orchestia ditmari* Derzhavin 1923, p. 187

Material examined

Southeastern Alaska: Bousfield & McAllister stn. A153, Mummy Is., Orca Inlet, 16 July 1961, 1 ♂ (16.0 mm), NMNS Cat. No. NMC-C-1981-580, slide mount; St. Paul Is., Bering Sea, July 1914, G.K. Parker coll., 5 ♂♂ (to 14.5 mm), 2 ♀♀ ov., NMNS Cat. No. NMC-C-1981-578, slide mounts.

Western Pacific: Southern Sakhalin Is., USSR, 4 September 1946, E.F. Gurjanova coll., 3 ♂♂ (to 18.5 mm), 4 ♀♀ (br. II, to 13.0 mm), Zool. Inst. No. 32/32313, slide mounts; Nosappu, Hokkaido, Japan, 21 June 1971, H. Morino coll., 3 ♂♂ (to 20.5 mm), 2 ♀♀ ov. (to 13.0 mm), NMNS Cat. No. NMC-C-1981-576, slide mounts.

Diagnosis

Male (15–20 mm). Medium to large, moderately apomorphic species characterized by: antenna 1, flagellum nearly equal to peduncle, 6–7 segmented; antenna 2 stout (not incrassate), flagellum 15–18 segmented. Mandibular left lacinia 4+-dentate, 5th tooth minute, occasionally lacking (especially in female); maxilliped palp normal, outer plate medium, apically rounded. Coxa 1 about $^1/_3$ masked by coxa 2; coxae 2–4 wider than deep, rounded below. Gnathopod 1, segment 4 lacking posterior tumescence or blister; dactyl slightly shorter than palm of propod; gnathopod 2, propod large, slightly broadening distally, palm gently convex, oblique. Peraeopod 4, segment 5 short (about $^2/_3$ segment 6), dactyl strongly pinched, nail long. Peraeopods 5–7, bases slightly dissimilar in shape, hind margin of 5 and 6 rounded, of 7 straight, weakly serrate; peraeopod 7 longest and slightly sexually dimorphic, segment 6 distally with longitudinal facial row of brush setae increasing in length distally, and short transverse apical row of 5–6 short setae. Abdominal side plates 2 and 3 deep, hind corners acute, hind margins weakly serrulate and setulose; pleopods much reduced, third shortest, rami 2–5 segmented, distinctly shorter than peduncles. Uropod 1, peduncular margins with 3–4 spines, inner ramus with 5–6 inner marginal and 3 outer marginal spines; outer ramus with 2–3 widely spaced marginal spines, not sexually dimorphic; uropod 2, outer margin of peduncle with 3–4 spines, heaviest distally; inner ramus with 2–3 inner and outer marginal spines; outer ramus with 2–3 outer marginal spines. Uropod 3, peduncle relatively shallow, with 3–4 mostly short posterior marginal spines; ramus much shorter, with short posterior marginal spines and longer apical spines. Telson lobes each with several dorsolateral spine groups and 3–4 apical spines of unequal size. Coxal gills 2 and 6 much the largest, 6 elongate, more than twice the length of gill 5.

Female (12–15 mm ov.). Gnathopod 1, palm distinct, with small posterodistal tumescence, exceeded by most of unguis of closed dactyl, posterior marginal spines short. Gnathopod 2, segment 2 widest proximally, segment 4 broadly tumescent behind, segment 5 deeply tumescent, 6 slightly shorter than 5. Brood plate margins subparallel, with about 40 long hook-tipped setae, mainly anteriorly. Peraeopod 5, length of brood plate about half that of gnathopod 2, margins 20-setose. Females are distinguishable from females of *T. traskiana* not only by the greatly reduced pleopod rami, but also by the longer antenna 1, smaller palm of gnathopod 1, longer and narrower brood plates, relatively longer peraeopods 5–7, with longer dactyls and less strongly convex posterior margins of bases.

Distributional ecology

Under drift-line debris, on sandy, rocky and stony beaches of exposed and semi-protected shores of the entire North Pacific rim region from Japan (north Honshu and Hokkaido) and Sakhalin in the west through Kamchatka, St. Paul Island to southeastern Alaska (Prince William Sound) in the east. Since the distribution of *Traskorchestia ochotensis* brackets the Aleutian Island chain, the records of Murie (1959) for "beach fleas" and "sand fleas" from that region very probably include this species also. Females ovigerous in May–July; apparently only one brood per year.

Remarks

Minor morphological variations occur in mature males and females throughout the range, but a 15.0 mm male from Orca Island, southeastern Alaska compares closely with a 15.0 mm subadult male from Noppura, Hokkaido. Mature males have a sexually dimorphic peraeopod 7 in which segment 4 broadens distally, the hind margin is arcuate, and segment 6 is bowed rather markedly, not straight. This species is not to be confused with the somewhat smaller *T. ditmari* Derzhavin (1923) that occurs along the shores of the Sea of Okhotsk in Kamchatka and the Kurile Islands (Derzhavin, 1937). Lack of material of *T. ditmari*

prevents critical evaluation of differences in females and mouthparts, pleopods, etc.; however, comparison on material of *T. ochotensis* (on hand) with the rather good drawings of Derzhavin (1923) has revealed species differences believed significant.

Paciforchestia new genus

Diagnosis

Medium to medium-large beach fleas, characterized by: smooth, unmodified bodies; eyes lateral, medium, not dorsally contiguous; inferior antennal sinus distinct, shallow; antenna 1 extending beyond peduncular segment 4 of antenna 2, peduncle 3 longest, flagellum upturned distally; antenna 2 slender, elongate, geniculate at flagellum, not incrassate (♂). Buccal mass directly beneath head, not very deep; mandible, left lacinia fully 5-dentate; right lacinia tricuspate; maxilliped palp obscurely 4-segmented (4th minute, masked by distal spines of 3), segment 2 broad, inner distal lobe large. Coxae 2–4 broad, rounded ventrally, cuspate posteriorly. Gnathopod 1 (♂), segments 4, 5 and 6 tumescent behind, palm not exceeded by dactyl; gnathopod 1 (♀) blister vestigial or lacking on segment 4; dactyl not exceeding palm. Gnathopod 2 (♂) powerfully subchelate, palm smoothly oblique, unguis of dactyl attenuate. Gnathopod 2 (♀), basis slightly to moderately expanded anteriorly, segment 3 slightly elongate, segments 4 and 5 with weak or low posterior blisters. Peraeopods 3 and 4 elongate, unequal, cuspidactylate, dactyls short, that of peraeopod 4 weakly pinched; peraeopod 4, segment 5 shorter than in peraeopod 3; peraeopods 5–7 homopodous, increasing posteriorly, bases rounded behind; coxa 5 anterolobate; peraeopod 7 sexually dimorphic in length but not in form. Abdominal side plates deep, weakly setulose behind, hind corners minutely acuminate. Pleopods more or less reduced, pleopod 3 shortest, rami shorter than peduncles, peduncular margins smooth, retinacula 2–8. Uropods 1 and 2 slender, rami and peduncles marginally spinose, peduncle 1 with laterodistal (inter-ramal) spine. Uropod 3, peduncle very deep, strongly spinose posteriorly, ramus shorter, spinulose posteriorly and apically. Telson long, narrowing, lobes separated near tip, with a few short apical spines, occasionally singly inserted dorsolateral spines. Coxal gills reduced, modified, that of peraeopod 6 elongate, sinuous. Brood plates large, subovate, marginal setae numerous, long, simple-tipped.

Type species: *Parorchestia klawei* Bousfield 1961

Additional species:

Paciforchestia pyatakovi (Derzhavin 1937), p. 89, fig. II(i)
See also Bulycheva, 1957, p. 172, figs. 62a, b, and Morino, 1975, p. 178, figs. 9–11

Paciforchestia tenuimana (Iwasa 1939), p. 268, pl. XIII, figs. 10–11

Etymology

The generic name is a combining form of *Orchestia* and the regional geographic name Pacific. Gender: Feminine.

Remarks

"Orchestia" *kokuboi* Ueno 1929 has many features of this genus, but the laterally plumose peduncles of the pleopods, short telson, and absence of a distolateral spine on uropod 1 are atypical. *Paciforchestia* is extremely plesiomorphic, little advanced beyond *Protorchestia* and members of the palustral group and primitive terrestrial Talitridae of the southern hemisphere. (Tables II, IV; figs. 26, 28)

Key to species of *Paciforchestia*

1. All pleopods much reduced, rami distinctly shorter than peduncle, 1–3 segmented; uropod 3, ramus slender, cylindrical, about $^2/_3$ peduncle length; telson lobes with apical spines only (rarely single dorsolateral spines) 2
   Only pleopod 3 much reduced, rami shorter than peduncle, 4–8 segmented; uropod 3, ramus short, subconical, about $^1/_2$ length of peduncle; telson lobes with 2 dorsolateral spine groups, plus apical spines ..... *P. klawei* (Bousfield) (p. 18)
2. Antenna 1, peduncular segment 3 distinctly ($^1/_3$) longer than peduncle 2, hind margin with small spines; uropod 1, outer ramus marginally smooth ..... *P. tenuimana* (Iwasa)
   Antenna 1, peduncular segment 3 slightly longer than peduncle 2, hind margin smooth; uropod 1, outer ramus distally with marginal spines ..... *P. pyatakovi* (Derzhavin)

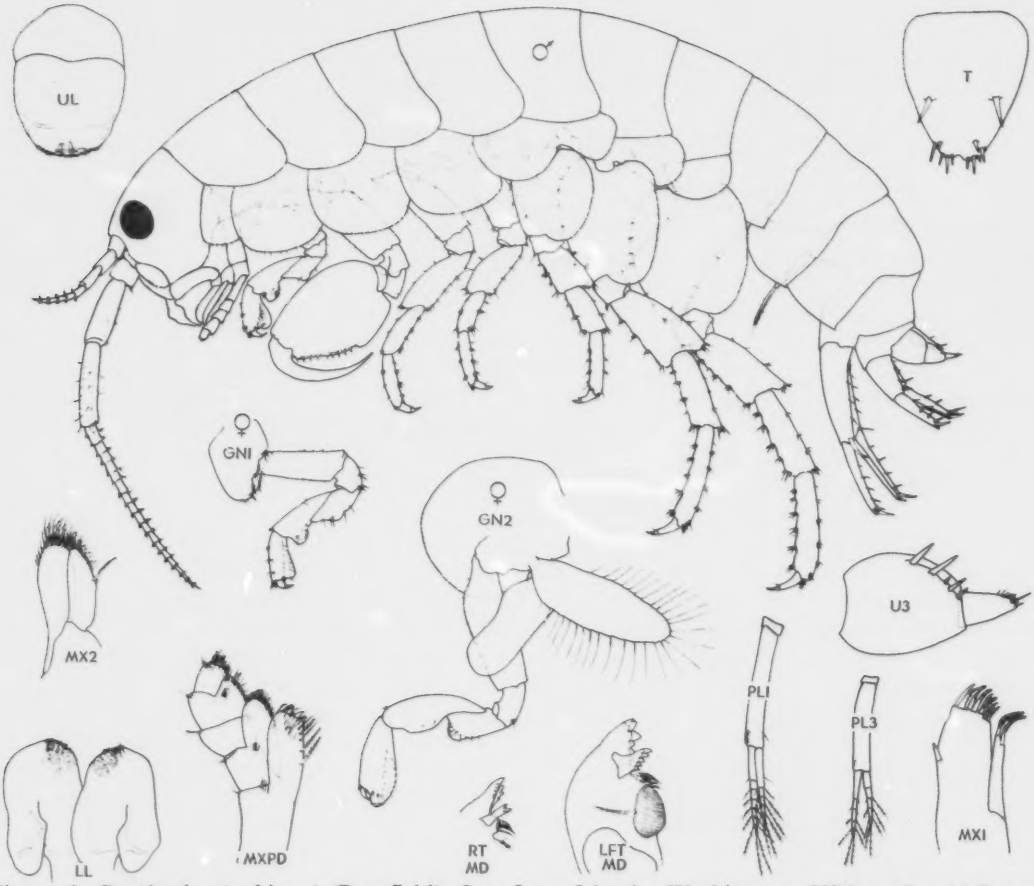

Figure 8. *Paciforchestia klawei* (Bousfield). San Juan Islands, Washington, USA. ♂ - 14.5 mm, ♀ ov. - 13.0 mm.

Paciforchestia klawei (Bousfield 1961)
Figure 8

Parorchestia klawei Bousfield 1961, p. 3, fig. 1, 2
:(?) Barnard, 1969b, p. 76, 221

Material examined

British Columbia: E.L. Bousfield 1955 stn. P6a, Wickininnish Bay, south end, fine sand at HW level, 2 August 1955, 1 imm. (5.0 mm); stn. M2, Emmond's Beach, near Powell River, pebble beach, HW level, 25 August 1955, 1 ♀ br. II (11.5 mm), NMC-C-1981-555, slide mount; Portland I. (48°43.5'N,123°22'W), intertidal, 15 June, 1927, 1 ♂ (14.5 mm), BCPM collections (courtesy P. Lambert).

Washington: San Juan Co.; Kiket Is., intertidal, 26 October 1968, Houghton coll., 2 ♂♂ (to 15.0 mm), 1 ♀ br. II (brood plate II stage) (to 14.0 mm), Friday Harbor Marine Laboratory collection, slide mounts. Goose Island, sand beach under gravel and *Fucus* mat (0–30 cm level), 26 April 1977. E. Kozlof student team B., 1 ♀ br. II, Friday Harbor Marine Laboratory collections.

Mexico: Los Coronados, off Baja California, 25 January 1957, W.L. Klawe coll., 2 ♂♂ (to 10 mm), 2 ♀♀, 1 ov. (to 10.0 mm). NMNS Cat. No. 6167, slide mount.

Diagnosis

As described originally. The smaller North American Pacific species differs from the two known large western Pacific species in a number of characters that *in toto* may be of subgeneric significance, viz: Antenna 1, peduncular segments 2 and 3 short, little longer than segment 1; gnathopod 2 (♂), palm with weakly defined hinge tooth; gnathopod 2 (♀) basis very slightly

expanded proximally, weakly arcuate posteriorly; coxae 2–4 medium deep, hind margin nearly vertical (versus sloped forward); coxa 5, anterior lobe moderately larger and deeper than posterior lobe; peraeopods 3–7, dactyls short, unguis not attenuated. Peraeopod 7 slightly longer than peraeopod 6 (versus much longer) in male. Pleopod rami multi-articulate, peduncles with 3–5 retinacula. Uropod 2, inner ramus with inner and outer marginal spines; uropod 3, ramus short and subconical versus slender-cylindrical. Telson broadly tapering, lobes with dorso-lateral and apical groups of spines, apical notch shallow. Coxal gills smaller, less strongly lobate or attenuated. Brood plates broader, marginal setae more numerous.

Remarks

This species complex encompasses plesiomorphic features of palustral and some terrestrial talitrids in the homopodous peraeopods; fully subchelate and palmate gnathopod 1 (both sexes); short dactyls, weakly "pinched" or incised peraeopod 4 dactyl; uropod 1 with distolateral peduncular spine; and elongate, weakly armed telson, but is distinguished by the 5-dentate left lacinia, cuspidactylate peraeopods, and deep peduncle of uropod 3.

Distribution ecology

Under drift debris on protected but bermless coarse sand and pebbly beaches, often with *Traskorchestia traskiana* and occasionally with *T. georgiana*, but usually much less abundant; throughout the Strait of Georgia, British Columbia (in summer-warm, slightly brackish areas only); also Santa Barbara, Southern California, to northern Baja California.

Transorchestia new genus

Diagnosis

Medium to medium-large smooth-bodied beach fleas, almost exclusively southern hemisphere, characterized by: eyes medium, lateral; antenna 1, peduncular segment 3 longest; antenna 2 sexually dimorphic, peduncle incrassate in male; inferior antennal sinus distinct, medium deep; buccal mass directly ventrally; mandibular left lacinia cleanly 4-dentate (rarely with 5th vestigial tooth), right lacinia tricuspate; maxilliped palp obscurely 4-segmented (4th minute, masked by spines of 3rd), segment 2 broad, with distinct medio-distal lobe. Gnathopod 1 (♂) deeply subchelate, palm much exceeding dactyl, segments 5 and 6 strongly, and 4 weakly tumescent behind; gnathopod 1 (♀) fully subchelate, dactyl slightly (or not) exceeding transverse palm, segments 4–6 lacking tumescent process; gnathopod 2 (♂), propod powerfully expanded, palm oblique, usually with stout (hinge) tooth, dactyl sinuous; gnathopod 2 (♀), basis little expanded, segment 3 short, 4 and 5 shallowly tumescent behind. Coxae 2–4 rounded ventrally, strongly cuspate behind. Peraeopods 3–7 cuspidactylate, dactyls short; peraeopod 4 shorter than peraeopod 3, segment 5 shorter, dactyl weakly pinched; peraeopods 5–7 weakly heteropodous, peraeopod 7 longest, peraeopods 6 and 7 sexually dimorphic in size and form; coxa 5 anterolobate, coxa 6 posterolobate, anterior margin of hind lobe nearly vertical. Abdominal side plates 2 and 3 weakly serrate behind, hind corners subacute; pleopods slender, normal (rami usually longer than peduncle), outer margin of peduncles very weakly spinose and/or lined with fine "fuzz" setae. Uropod 1, peduncular distolateral (inter-ramal) spine not developed, rami weakly marginally spinose; uropod 2, inner ramus, both margins spinose. Uropod 3, peduncle deeply broadened, posterior margin short-spinose; ramus short. Telson elongate, tongue-shaped, lobes distally narrowing, separated apically, each with long dorsolateral marginal row of short stout spines, and apical spines. Coxal gills 3–5 somewhat reduced, those of peraeopod 2 and peraeopod 6 large and bladder-like. Brood plates (♀) broadly subovate, margins with numerous long hook-tipped setae.

Type-species: *Orchestia chiliensis* Milne-Edwards 1840

Additional species: *Transorchestia serrulata* (Dana 1852)

Transorchestia enigmatica (Bousfield & Carlton 1967)

Transorchestia chiliensis gracilis (Chilton 1920); Hurley, 1957, p. 160

Transorchestia miranda (Chilton 1916); Hurley, 1957, p. 162, figs. 4, 5

Transorchestia sp. (Australian species, Bousfield, (in prep.)[1]

(?)*Transorchestia bollonsi* (Chilton 1909); Hurley, 1957, p. 160, fig. 3; Bousfield, 1964, p. 54, fig. 5

[1]Bousfield, E.L. A revised classification of Talitrid amphipods (Crustacea: Amphipoda: Talitridae). (In prep.)

Etymology
The generic name reflects its phyletically intermediate position between the most primitive and most advanced members of the beach flea genus *Orchestia* (sens. lat.) Gender: Feminine.

Remarks
The four species and subspecies of the *chiliensis* complex are herewith maintained as separate entities pending study of more extensive material from South America, Australia, New Zealand, and other land masses of the southern hemisphere. *T. bollonsi* from the subantarctic islands of New Zealand is tentatively included in this group despite its special morphological features (reduced pleopod rami, knob-like brood plate setae, short palm of gnathopod 1 (♀), and more heavily spinose uropod rami). The full species groups may be separated according to the following key. The genus appears intermediate between the plesiomorphic *Traskorchestia* and the more apomorphic *Orchestia* sens. str., and may be antecedent to the latter, hence the name *Transorchestia*. (Tables II, IV; figs. 26, 28)

Key to described species of *Transorchestia*

1. Uropod 3, ramus sublinear, nearly equal to peduncle; gnathopod 1 (♀), palm short, distinctly exceeded by dactyl; pleopods reduced, rami distinctly shorter than peduncle; brood plate setae club-tipped ..... *Transorchestia bollonsi* (Chilton)
   Uropod 3, ramus subconical, much shorter than peduncle, gnathopod 1 (♀), palm little (or not) exceeded by dactyl; pleopods normal, rami not shorter than peduncles; brood plate setae hook-tipped 2
2. Gnathopod 2 (♂), palm smooth, convex, lacking well-defined hinge tooth; peraeopod 7 (♂) segment 5 strongly broadened posteriorly, width nearly equal to length ..... *T. miranda* (Chilton)
   Gnathopod 2 (♂), palm concave posterior to strong hinge tooth; peraeopod 7 (♂) segment 5 less strongly inflated, width about $^2/_3$ length ..... *T. chiliensis* group (p. 20) (comprises *T. chiliensis* (Milne-Edwards), *T. serrulata* (Dana), *T. enigmatica* (Bousfield & Carlton), and *T. chiliensis gracilis* (Chilton)).

Transorchestia chiliensis (Milne-Edwards 1840)
Figure 9

Orchestia chiliensis Milne-Edwards 1840, p. 18
:Stebbing, 1906a, p. 537
:Ruffo, 1949, p. 53, fig. 18
non *Orchestia chiliensis*: Hurley, 1957, p. 157, fig. 2

Material examined
Cape Horn region, South America, Hudson 70 Expedition: E.L. Bousfield stn. F.1, Puerto Robalo, Isla Navarino, Chile (54°57'S,67°40'W), 29 January 1970, 7 ♂♂ (to 14.5 mm), 11 ♀♀ (7 ov.) 3 juv.; stn. F.14, Playa Aaron, Isla Navarino, 5 February 1970, 2 ♂♂; stn. F.17, Cabo Maria, Isla Navarino, 7 February 1970, 3 ♂♂, 5 ♀♀ (ov.), 3 juv., stn. F.20, Peninsula Scott, west beach, Isla Navarino, 10 February 1970, 7 ♂♂, 12 ♀♀, 16 juv.; stn. F.34, Punta Zegers, Tierra del Fuego, Chile, 22 February 1970, 19 ♂♂ (to 16.0 mm), 11 ♀♀ (ov.) (to 13.0 mm), 3 juv. NMNS collections, slide mounts.

Diagnosis
Male (14.0–16.0 mm). A medium-sized, stout-bodied species, closely agreeing with the description and figures of Ruffo (1949), but somewhat less well with "*O. chiliensis*" (probably *O. serrulata* Dana) as described and figured in detail by Hurley, 1957 (above). Distinctive features are: antenna 1, peduncular segment 3 often with 2 posterior marginal spines, and segment 1 with posterodistal spine (rather than setal group); antenna 2, segments 4 and 5 stoutly incrassate, flagellum 17-segmented. Gnathopod 1, segment 4 with weak but distinct posterior blister; gnathopod 2, basis not noticeably expanded or serrate antero-distally; propod, palmar hinge tooth very prominent, posterior sinuous bulge of dactyl about mid-point, closing on palm just below hinge tooth; peraeopod dactyls very short, relatively thick proximally, outer margin convex, unguis very short; dactyl of peraeopod 4 very short, nail about $^1/_2$ dactyl body length. Peraeopods 6 and 7, segments 4 and 5 strongly incrassate, width more than $^1/_2$ length, broader

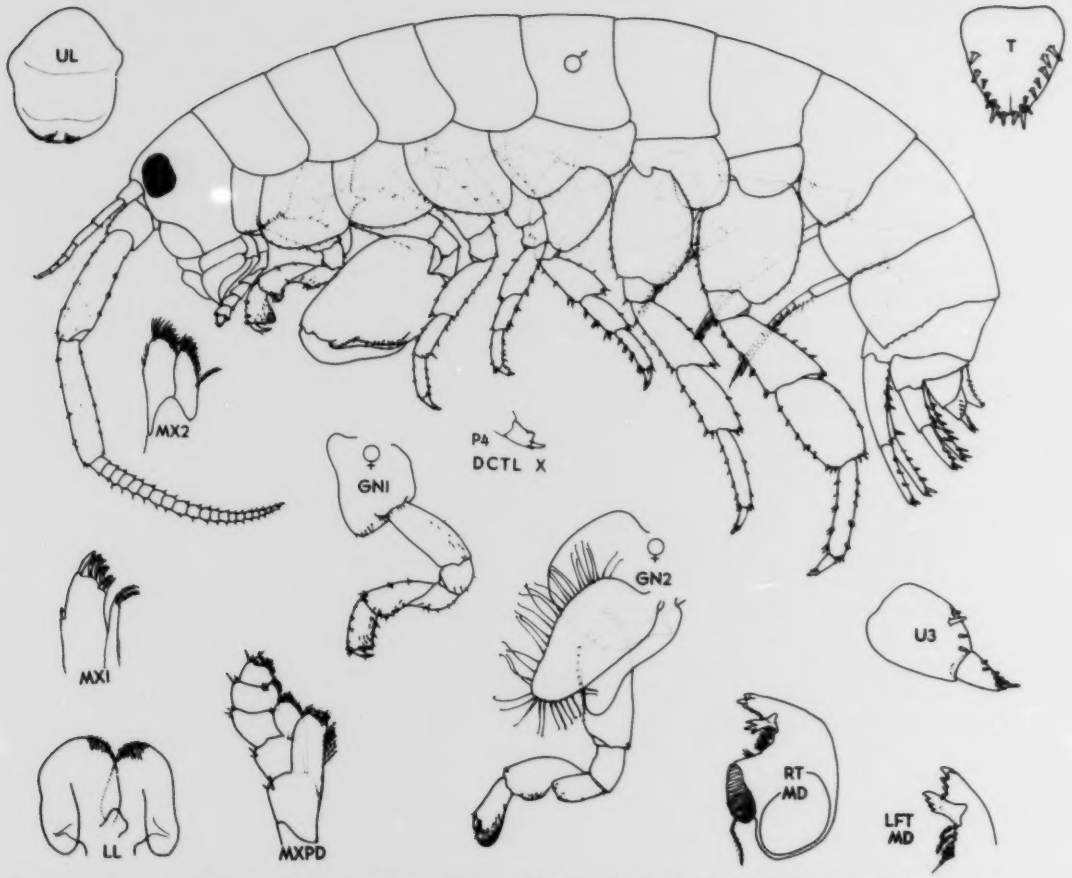

Figure 9. *Transorchestia chiliensis* (Milne-Edwards). Puerto Robalo, Chile. ♂ - 15.0 mm, ♀ ov. - 12.0 mm.

on peraeopod 7. Pleopods 1, 2 and 3, peduncles with 1, 2 and 3 outer marginal short spines, and fine fuzz setae, barely visible on 1. Uropod 2, inner ramus with 2 medial marginal and 1 lateral marginal spines respectively. Uropod 3, basis with 5 posterodistal spines, middle spine the largest. Telson lobes each with about 6 dorsolateral spines, proximal 1st and 3rd largest, and 2 unequal apical spines.

Female (12.0 mm, ov.). Gnathopod 2, basis relatively short and broad, anterior margin very slightly indented distally, lined with 6–7 well-spaced spinules. Brood plate of peraeopod 2 broadest near base, anterior margin with about 30, and posterior margin distally with about 10, long hook-tipped setae.

Remarks

Mature males of *O. chiliensis* differ from similar-sized rocky-shore specimens from Portobello, New Zealand, in the shorter but more spinose antenna 1, longer flagellum of antenna 2, more proximal sinuosity of the dactyl of gnathopod, relatively short, bowed dactyls of peraeopods, slightly more spinose pleopod peduncles, and slight but consistent differences in armature of uropods and telson. In comparable female material from New Zealand, the basis of gnathopod 2 is relatively longer, the anterior margin more strongly incised, and the brood plates of peraeopod 2 have about 25 and 15 hook-tipped setae on anterior and posterior margins respectively.

Transorchestia enigmatica (Bousfield & Carlton 1967)
Figure 10

Orchestia enigmatica Bousfield & Carlton 1967, p. 278, figs. 1, 2
Orchestia chiliensis: Bousfield, 1975, p. 363, fig. 234a, b

Material examined
Lake Merritt, Oakland, Alamedo Co., California, among tubes of *Mercierella enigmatica*, 17 June 1965, J. Carlton coll., 1 ♂ (15.5 mm), Paratype, USNM File No. 260765, slide mount (in NMNS, Ottawa). Type and paratype material from Lake Merritt, NMC-C-1981-53,532.

Distributional ecology
Intertidally under damp rotting wood, leaves, and other organic debris, and occasionally among the tubes of *Mercierella enigmatica* Fauvel, around the brackish-water margins of Lake Merritt, the levels of which fluctuate according to the flood gate. Females ovigerous in summer (June to August).

Remarks
The species has been recorded to date only from the shores of Lake Merritt, within the city of Oakland, California. After further examination of fully mature males, the species was assigned to *O. chiliensis* by Bousfield (1975). However, careful comparison of all material of *T. enigmatica* from Lake Merritt with extensive series of *T. chiliensis* from the Cape Horn region (the general type-locality) reveals consistent differences, especially in the longer, more slender peraeopod dactyls, more narrowly ovate female brood plates with more numerous posterior marginal setae, more distal location of posterior marginal bulge of the dactyl of gnathopod 2 (♂), and minor differences in the form and armature of uropod 3 and telson. These differences indicate that *T. enigmatica* is distinct from rocky shore material of *T. chiliensis* sens. str., especially from the Cape Horn region. However, comparison of mature male and female specimens of *T. enigmatica* with similar-sized material from a salt-marsh near Miranda, North Island, New Zealand, E.L. Bousfield collector, October 1978 (cf. Paviour-Smith, 1956), yields closer agreement in: less incrassate antennae and peraeopods 6 and 7; more attenuated, slender peraeopod dactyls; more strongly spinose peduncles of pleopods 2 and 3, and more similar armature of uropod 3 and telson. In Miranda marsh females, however, the brood plate of gnathopod 2 is less broad, and the anterior and posterior margins have 23 and 15 hook-tipped setae respectively. *T. chiliensis gracilis* Chilton from Juan Fernandez, is a terrestrial species, shows several distinctive morphological features of gills and gnathopods, and is almost certainly a valid full species. Although the probability is high that *T. enigmatica* is conspecific with one of these (or an undescribed) species or forms from the southern hemisphere, the species name is herewith retained pending study of more extensive materials from all pertinent regions.

Orchestia Leach 1813–14

Diagnosis
The genus *Orchestia* has been more narrowly redefined by Bousfield (in prep.)[1] to encompass the type group of shore-dwelling and immediate "coastal terrestrial" species of the Atlantic–Mediterranean region (e.g., of Karaman, 1970), with the following primary characteristics: body smooth, medium to medium-large. Eyes lateral, not enlarged or dorsally contiguous. Inferior antennal sinus distinct, medium deep. Antenna 1 short, peduncular segment 3 not longer than 2, bare; antenna 2 usually sexually dimorphic. Buccal mass slightly prognathous, mandibular left lacinia cleanly 4-dentate, rarely with vestigial 5th tooth; maxilliped palp 3-segmented, segment 2 broad, with distinct, medio-distal lobe. Gnathopod 1 (♂) fully subchelate, palm little exceeding dactyl, segments 5 and 6 (but not 4) tumescent; gnathopod 1 (♀), segment 5 slender, dactyl distinctly exceeding short palm, segments 4–6 lacking tumescent process. Gnathopod 2 (♂), propod powerful, palm oblique, usually with tooth, dactyl usually sinuous; gnathopod 2 (♀), basis broadly expanded anteriorly, segment 3 short, 4 not tumescent posteriorly. Peraeopods 3–7 cuspidactylate, peraeopod 4 shorter than 3, segment 5 shorter, dactyl distinctly pinched.

[1]Bousfield, E.L. A revised classification of Talitrid amphipods (Crustacea: Amphipoda: Talitridae). (In prep.)

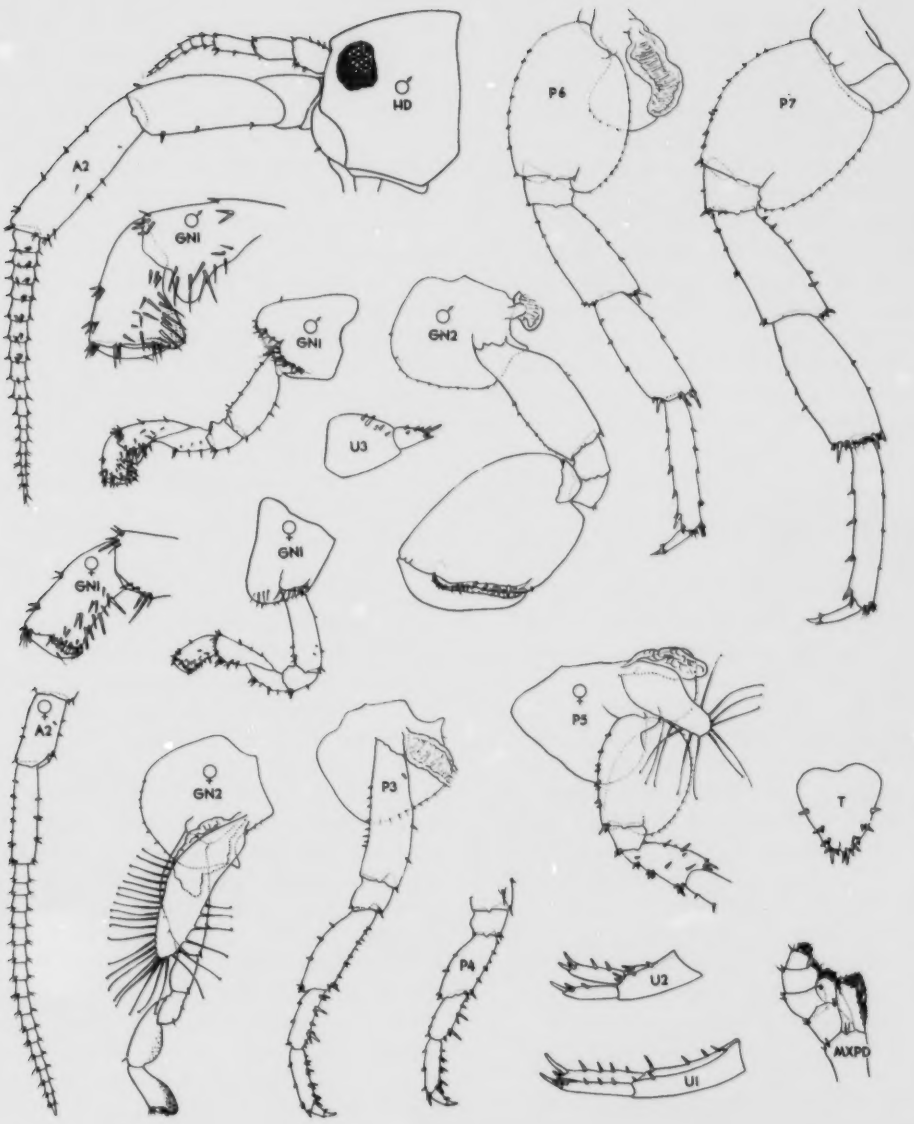

Figure 10. *Transorchestia enigmatica* (Bousfield & Carlton). Lake Merritt, Oakland, California. ♂ - 11.5 mm; 2 ♀ ov. - 11.0 mm. (Recomposed from Bousfield & Carlton, 1967).

Peraeopods 5–7 weakly heteropodous, dactyls slender; peraeopod 7 longest, usually sexually dimorphic in form and size; coxa 5 anterolobate, 6 posterolobate, hind lobe oblique, anterodistally rounded. Abdominal side plates 2 and 3 weakly crenulate behind, posterior corner acute, lower face not pitted. Pleopods slender, normal or slightly reduced; peduncles 2 and 3 very weakly

spinose, lacking fine setae, each with 2 retinacula. Uropods 1 and 2, peduncle with distolateral spine weak or lacking, rami marginally spinose, both margins of inner ramus spinose. Uropod 3, peduncle not strongly broadened; ramus short, tapering. Telson not elongate, lobes with dorsolateral and apical spine groups, weakly notched or separated apically. Coxal gills 3–5 reduced. Brood plates large, narrowly ovate; marginal setae numerous, simple.

Type-species: *Oniscus gammarellus* Pallas 1766 (monotype and subsequent synonymy)

The group comprises about 15 mostly Mediterranean–Atlantic species including *O. montagui* (Audouin 1826), *O. mediterranea* Costa 1857, *O. cavimana* Heller 1865, *O. gambierensis* Chevreux 1908, *O. magnifica* Vecchi 1931, *O. remyi* Schellenberg 1950, + subspecies *roffensis* Wildish 1968, *O. grillus* Bosc 1802, *O. stephenseni* Cecchini 1928, *O. kosswigi* Ruffo 1949 and *O. microphtalma* Amanieu & Salvat 1963, (See also Karaman, 1970).

Section II. Sandhoppers (substrate modifiers, *sensu* MacIntyre, 1963)

Recent revision of world sandhoppers (Bousfield, in prep.)[1] has subdivided the group primarily on the basis of dentition of the mandibular left lacinia mobilis. This character is somewhat variable within the two groups and not absolutely taxonomically critical, reflecting the extreme difficulty of defining natural groups on a rigid taxonomic basis, and advisability of the character consensus approach to natural groupings. Thus, dentition of the left lacinia mobilis tends to be strongly correlated with certain conditions of other morphological characters, as follows:

4-dentate group

Body generally stout, surface occasionally rugose or ridged. Eyes medium to moderately enlarged, not contiguous mid-dorsally. Antenna 2 short, especially in female, seldom sexually dimorphic in form; buccal mass directly ventral; mandibular left lacinia 4-dentate, rarely 5-dentate. Coxae 2–4 deep, weakly or not cuspate behind. Gnathopod 1 (♂) often fully subchelate, dactyl exceeding palm. Gnathopod 1 (♀), palm small or lacking. Gnathopod 2 (♀), basis little expanded anteriorly, segment 4 rarely tumid or processiferous behind. Coxa 5 aequilobate, coxa 6 strongly and deeply posterolobate, anterior margin vertical. Uropod 3 short, ramus tapering (seldom compressed), rarely longer than peduncle or sexually dimorphic. Telson very short and broad, lobes fused at apex, rarely with dorsal spines (marginal only). Coxal gills relatively large, 3–5 not markedly smaller than 2 and 6; brood plates broadly ovate, large on peraeopod 5.

Composition

Orchestoidea Nicolet (sens. str.), "*Orchestoidea*" *brasiliensis* (Dana 1853), *Talitrus saltator* Montagu 1808, and most sand beach hoppers of southern Australia–New Zealand and South Africa (e.g., of Hurley, 1956).

5-dentate group

Body stout or slender, surface usually smooth. Eyes medium to very large, often nearly contiguous mid-dorsally, often sexually dimorphic. Antenna 2 relatively long, usually strongly sexually dimorphic, peduncle often incrassate in male; mandibular left lacinia usually cleanly 5–6 dentate, seldom with 5th (proximal) tooth vestigial or lacking. Coxae 2–4 often as broad as deep, usually strongly cuspate behind. Gnathopod 1 (♂) seldom fully subchelate, palm usually vestigial or lacking. Gnathopod 1 (♀) palm usually lacking, very short when present. Gnathopod 2 (♀), basis more or less strongly expanded anteriorly, segment 4 often with posterior process. Coxa 5 anterolobate; coxa 6 posterolobate, lobe often shallow, anterior margin often oblique. Uropod 3 various, ramus usually longer than peduncle, often laterally compressed, occasionally sexually dimorphic. Telson lobes more elongate, often separated apically, bearing dorsal and apical spines. Coxal gills strongly reduced, those of peraeopods 3–5 small. Brood plates elongate ovate, variable in length, occasionally lacking, that of peraeopod 5 short, weakly setose.

Composition

Platorchestia new genus (partim), *Megalorchestia* Brandt, *Trinorchestia* new genus, *Pseudorchestoidea* new genus, *Talorchestia* Dana, most species of the Indo-Pacific and northern hemisphere and new generic groups proposed by Bousfield (in prep.)[1].

[1]Bousfield, E.L. A revised classification of Talitrid amphipods (Crustacea: Amphipoda: Talitridae). (In prep.)

Key to genera of sandhoppers of the North Pacific rim region and selected world-wide genera

1. Mandibular left lacinia basically 4-dentate (fig. 1d); gnathopod 2 (♀) basis sublinear, little expanded anteriorly (fig. 2n); uropod 3 short, ramus cylindrical or tapering, not longer than peduncle (figs. 1i, j); telson short, broad, entire, with marginal spines only (fig. 1p) 2
   Mandibular left lacinia basically 5-dentate; gnathopod 2 (♀) basis more or less strongly broadened anteriorly (fig. 2p); uropod 3 medium to elongate, ramus usually laterally compressed, longer than peduncle; telson as long as broad, with dorsal and marginal spines (fig. 1o) 4
2. Gnathopod 1 distinctly subchelate in male, often very weakly so in female (figs. 2a, g) ..... Most "Talorchestia" species of the southern hemisphere
   Gnathopod 1 lacking distinct palm in male and female (Figs. 2b, c, d, h) 3
3. Gnathopod 2 (♂) powerfully subchelate; pleopods reduced, peduncles widened, outer margin strongly long-spinose (fig. 3q); uropod 3, apical spines numerous, short ..... *Orchestoidea* Nicolet (p. 43)
   Gnathopod 2, propod small, mitten-shaped in male (as in female and imm.); pleopods normal, rami long, peduncles slender, outer margin short-spinose (fig. 3p); uropod 3, ramus with single long apical spine ..... *Talitrus* Latr. (p. 45)
4. All pleopod peduncles spinose along entire outer margin (figs. 3n, p); uropod 1, peduncle and outer ramus always stoutly marginally spinose (fig. 3g) 5
   Pleopod peduncles, especially pleopod 1, outer margin not spinose or only partly so; uropod 1, peduncle and outer ramus weakly or not spinose marginally (fig. 3f) 6
5. Pleopod rami very reduced, much shorter than peduncles; peduncles basally broadened, marginal spines long, strong (fig. 3r); gnathopod 1 (♂ and ♀), propod long, tapering distally, length greater than ½ anterior margin of carpus (figs. 2d, h) ..... *Megalorchestia* Brandt (p. 29)
   Pleopod rami not reduced, multi-segmented; peduncles linear, marginal spines short (fig. 3p); gnathopod 1 (♂ and ♀), propod short, stout, length about ½ anterior margin of carpus (fig. 2b) ..... *Trinorchestia* new genus (p. 41)
6. Peraeopod 5 much smaller than peraeopods 6 and 7 and differing markedly in form of basis and segment 4 (fig. 3n); peraeopod 5 dactyl short, thick, nail vestigial; gnathopod 1 (♂), propod totally lacking palmar margin between posterodistal blister and unguis (fig. 2c); uropods 1 and 2, rami usually with terminal spade spines (fig. 3f). Mandibular left lacinia, 5th (proximal) tooth vestigial or lacking ..... *Pseudorchestoidea* new genus (p. 47)
   Peraeopod 5 smaller than, but similar in form to peraeopods 6 and 7 (fig. 3m); peraeopod 5, dactyl normal, nail elongate; gnathopod 1 (♂) more or less subchelate, propod with short, distinct palm (fig. 2a); uropods 1 and 2, terminal spines regular, acute-tipped (fig. 3c). Mandibular left lacinia cleanly 5-dentate 7
7. Gnathopod 1, propod with distinct palm, dactyl of female exceeding, dactyl of male little or not exceeding, palm; coxa of peraeopod 6, posterior lobe, anterior margin vertical, often with distinct distal process (fig. 3j); antenna 2 and peraeopod 7 strongly sexually dimorphic in form, some segments incrassate or broadened in male (figs. 3c, k) ..... *Platorchestia* new genus (p. 26)
   Gnathopod 1, propod with small but distinct palm only in male, always exceeded by dactyl; coxa of peraeopod 6, hind lobe rounding anterodistally, margin usually oblique; antenna 2 and peraeopod 7 (in male) elongate but not differing in form from female ..... *Talorchestia* Dana

Platorchestia new genus

Diagnosis

Medium-sized, smooth-bodied, semi-fossorial talitrids, little evolved from the "beach flea" facies (relatively weakly spinose appendages), characterized by: antenna 1 short, not exceeding peduncle 4 of antenna 2, peduncular segments subequal; antenna 2 short, sexually dimorphic (peduncle usually strongly incrassate in male); inferior antennal sinus shallow, distinct; eyes medium to small, vertically subrectangular, quadrate to round. Buccal mass directly beneath head; left mandibular lacinia cleanly 5-dentate; maxilliped palp relatively short, broad, obscurely 4-segmented, segment 2 strongly spinose medially, with mediodistal lobe, segment 3 rounded apically, spines masking minute 4th segment. Coxa 1 shallow, shorter than cuspate coxae 2–4, anterodistal border rounded, not sharply acute. Gnathopod 1 (♂) distinctly subchelate, dactyl equal to or slightly exceeding palm, propod not narrowing distally, carpus not elongate, segments 5 and 6 with posterior tumescence; gnathopod 1 (♀), propod with short palm, greatly exceeded by dactyl, segments 4–6 not tumescent behind; gnathopod 2 (♂) powerfully subchelate, palm nearly vertical, notched or sinuous, dactyl stout; gnathopod 2 (♀), basis broadened anteroproximally; segment 3 short, segment 5 (not 4) shallow-tumescent posteriorly, segment 6 shorter than carpus. Peraeopods 3–7 cuspidactylate, nails short. Peraeopods 3 and 4 unequal; in peraeopod 4, segment 5 often very short (width nearly equal length), body of dactyl usually strongly pinched or sharply constricted; peraeopods 5–7 more or less similar in form, increasing in length posteriorly, bases rounded behind, peraeopod 7 (and often peraeopod 6) sexually dimorphic in form, segments 4 and 5 incrassate in male; coxa 5 anterolobate; coxa 6, hind lobe nearly vertical, antero-distal corner right-angled, or with short distal process. Abdominal sideplates 1–3, hind margin weakly serrulate, hind corners acute; pleopods normal, linear, outer margins of peduncles 2 and 3 weakly spinulose, inner with 2 retinacula. Uropods short, not heavily spinose; uropod 1, distolateral (interramal) spine not developed, outer ramus marginally bare or nearly so, terminal spines long; uropod 2, inner ramus spinose on inner and outer margins. Uropod 3, peduncle moderately broad, spinose posteriorly; ramus shorter than peduncle, with short posterior and apical spines. Telson short, lobes distally rounded, with dorsal and apical spine groups. Coxal gills reduced, especially on peraeopods 3–5, 2 and 6 longest. Brood plates (♀), elongate-ovate, smallest on 5, marginal setae long, simple-tipped.

Type-species: *Orchestia platensis* Krøyer 1845; Bousfield, 1973, p. 160, plate 46(2)

Additional species[1]

Platorchestia crassicornis (Derzhavin) 1937
:Bulycheva, 1957, p. 159, figs. 56a, b, (as *O. platensis*)
:Morino, 1975, p. 127, figs. 4–5 (as *O. platensis*)

Platorchestia pachypus (Derzhavin) 1937, p. 91, pl. 2, fig. 3, pl. 3, fig. 2
:Bulycheva, 1957, p. 146, fig. 52
:Morino, 1975, p. 179, figs. 4–6

(?) *Platorchestia zachsi* (Derzhavin) 1937, p. 90, pl. 2, fig. 2.
:Gurjanova, 1951, p. 811, fig. 565
:Bulycheva, 1957, p. 146, fig. 53

(?) *Platorchestia chathamensis* new species (p. 27)

(?) *Platorchestia japonica* Tattersall 1922
:Morino, 1975, p. 175

Etymology

The generic name, *Platorchestia*, is a combining form of *Orchestia* and the type-species name *platensis*. Gender: Feminine.

Remarks

This genus differs from *Orchestia* (sens. str.) mainly in the generally more spinose appendages; powerfully incrassate antenna 2 (♂); 5-dentate left mandibular lacinia; very short segment 5 of peraeopod 4; right-angled and processiferous hind lobe of coxa 6; marginally unarmed (or weakly armed) outer ramus of uropod 1; more heavily spinose pleopod peduncles, and smaller, less marginally setose brood plates. Members of the genus are restricted to the North Pacific (especially western shores); however, *P. platensis* (Krøyer) is nearly cosmopolitan along tropical-temperate coastlines, but has not yet been recorded from the eastern Pacific. Most members of the group demonstrate some fossorial behaviour and frequently occur on sandy beaches, often as pioneer species, before more specialized

[1] "*Talorchestia*" *fritzi* Stebbing 1903 from the Pacific coast of Costa Rica and Galapagos (see Shoemaker, 1932, and Monod, 1970) is closely allied here, but is tentatively retained in the Caribbean group of *Talorchestia* Dana.

burrowing talitrids take over. The *Platorchestia* group appears to be a north-temperate counterpart of the tropical Indo-Pacific plesiomorphic *Talorchestia* group, both of which burrow shallowly, and are likely precursors of more specialized substrate-modifying groups. *Platorchestia* is relatively apomorphic when grouped with the beach fleas (allied to *Orchestia*), but very plesiomorphic relative to the sandhoppers (near *Talorchestia*) (Tables II, III, IV; figs. 26, 27, 28).

Key to known species of *Platorchestia*

1. Coxal plate 5, hind lobe with distinct anterodistal process (fig. 3j); uropod 3, ramus nearly equal in length to peduncle, with 1–4 posterior marginal spines as well as apical spines; gnathopod 2 (♀), basis strongly broadened anteriorly 2
   Coxa 5, posterior lobe lacking distinct anterodistal process, lower margin meeting anterior margin nearly directly at right angle; uropod 3, ramus distinctly shorter than peduncle, with apical spines only; gnathopod 2 (♀), basis moderately expanded anteriorly (fig. 2o) 4
2. Eyes vertically subrectangular; gnathopod 1 (♂), dactyl nearly equal to total palm (including blister); gnathopod 2 (♂), palm medially notched; peraeopod 7 (♂), segment 5 moderately expanded, width not greater than half length; telson apically notched 3
   Eyes subovate; gnathopod 1 (♂), dactyl distinctly shorter than total palm; gnathopod 2 (♂), palm sinuous; peraeopod 7 (♂), segment 5 very broadly expanded, width equal to or greater than length; telson lobes separated in distal $^1/_3$ to $^1/_2$ ..... *P. pachypus* (Derzhavin)
3. Gnathopod 1 (♂), carpus elongate, anterior margin about $1^1/_2$ times propod; gnathopod 2 (♂) palmar notch medial; uropod 1, outer ramus usually with 1 marginal spine ..... *P. crassicornis* (Derzhavin)
   Gnathopod 1 (♂), carpus normal, anterior margin slightly longer than propod; gnathopod 2 (♂), palmar notch nearer posterior angle; uropod 1, outer ramus lacking marginal spine(s) ..... *P. platensis* (Krøyer)
4. Pleopods reduced, rami 3–4 segmented, distinctly shorter than peduncle; eye small, rounded ..... *P. chathamensis* new species (p. 27)
   Pleopods normal, rami multi-segmented, only slightly shorter than peduncle; eye normal, subquadrate 5
5. Gnathopod 1 (♂) neotenically arrested at half transformed stage (fig. 2l); antenna 2 (♂), peduncle strongly incrassate; uropod 1, outer ramus with marginal spines; seashore species ..... *P. zachsi* (Derzhavin)
   Gnathopod 1 (♂) fully powerfully subchelate, palm convex (fig. 2i); antenna 2 (♂), peduncle only slightly broader than in female; uropod 1, outer ramus marginally bare; terrestrial species ..... *P. japonica* (Tattersall)

Platorchestia chathamensis new species
Figure 11

Material examined

Chatham Island, near Victoria, B.C. among logs, at HW drift line, 4 July 1959, E.L. Bousfield and G.C. Carl coll., 1 ♀ ov. Holotype NMC-C-1981-509.

Diagnosis

Female (9.0 mm, ov.). A relatively small, apomorphic, somewhat aberrant species, tentatively assigned to this genus (in absence of male specimens to complete diagnosis). Eye small, rounded. Antenna 1, flagellum $3^1/_2$-segmented, much shorter than peduncle. Antenna 2 very short, appearing damaged or regenerating in single female specimen available. Buccal mass appearing slightly prognathous. Mandibular left lacinia, proximal (5th) tooth small. Maxilliped palp relatively short, broad, segment 3 short, rounded distally, 4th segment minute but not fused to 3rd. Gnathopod 1, carpus not elongate; propod palm very short, oblique, dactyl with single stout posterior seta; gnathopod 2, basis relatively little expanded anteriorly, broadest medioproximally; segments 4 and 5 shallow-tumescent behind. Peraeopod 4, dactyl

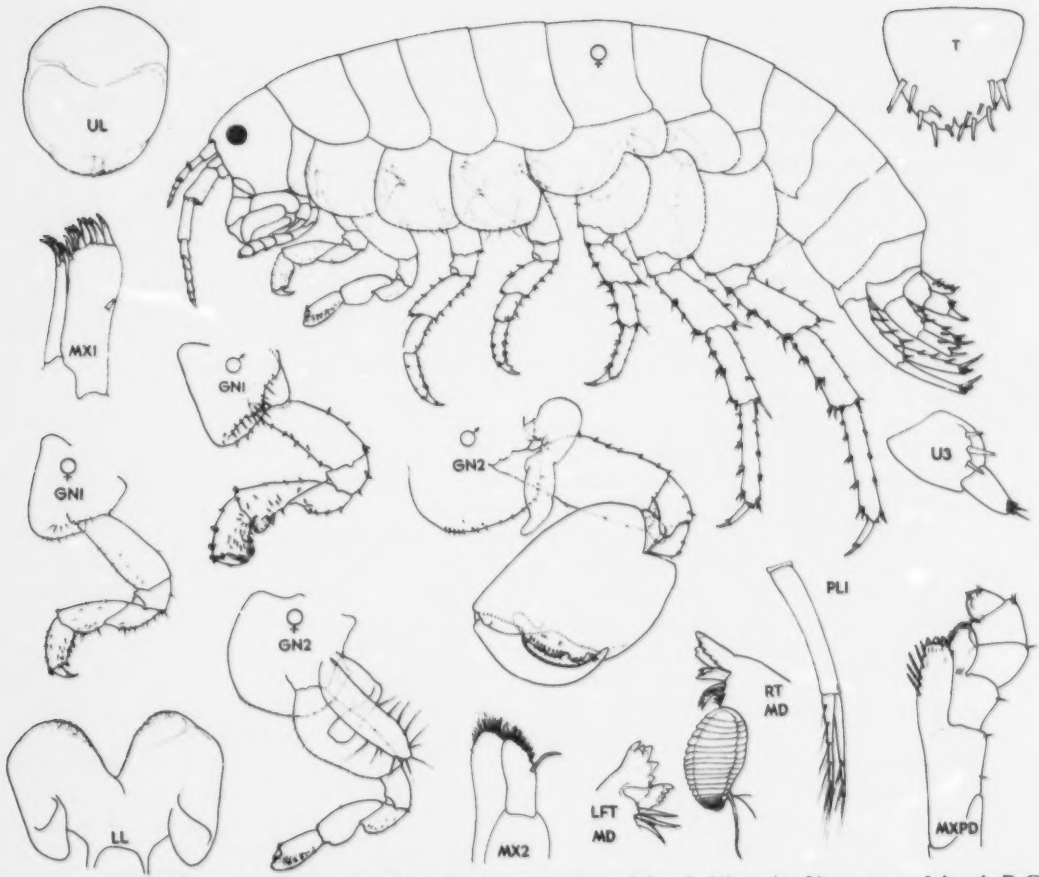

Figure 11. *Platorchestia chathamensis* new species. Chatham Island, Victoria, Vancouver Island, B.C. ♀ ov. - 9.0 mm. *P. platensis* (Krøyer). Nova Scotia. ♂ - 12.0 mm gnathopods.

weakly constricted, nail long. Peraeopods 5–7, slender, bases subsimilar, posterior margins convex, weakly crenulate; dactyls relatively long, slender; coxa 6, hind lobe without anterodistal process, lower margin slightly sinuous. Abdominal side plates 1–3, hind corners acuminate. Pleopods slender, distinctly reduced, rami 3–4 segmented, much shorter than peduncles; peduncles 1, 2 and 3 with 0, 2 and 4 outer marginal short spines respectively. Uropods 1 and 2 weakly spinose; uropod 1, outer ramus marginally bare, inner ramus with 2–3 inner and outer marginal short spines. Uropod 3 short, peduncle with 3 stout posterior marginal spines; ramus distinctly shorter than peduncle, subconical, with apical spines only. Telson lobes fused almost to apex, each with apical spines and 2 groups of dorso-lateral spines. Coxal gills relatively large, lobate (?). Brood plates 2–4 broadly sublinear, each with about 12 marginal simple setae, brood plate of peraeopod 5 very short, spade-shaped with 3–4 apical simple setae.

Remarks

The single female specimen is unlike all other known 5-dentate "Orchestia" species in characters above and in the key, and is herewith considered a distinctive new species. The overall facies is reminiscent of *Orchestia microphtalma* Amanieu & Salvat 1963, a log-burrowing species from the Atlantic coast of France; these similarities include the small rounded eye, short antenna 2 and reduced pleopods. However, the latter species is a true 4-dentate *Orchestia*, with more strongly spinose appendages, including marginally spinose outer ramus of uropod 1, posteriorly spinose ramus of uropod 3, and shorter peraeopod dactyls, among other differ-

ences. The single female of *P. orientalis* bears a superficial resemblance to ecologically associated females of *Traskorchestia* spp., but is excluded from that genus by the more minute maxilliped palp segment 4, the expanded basis of gnathopod 2 (♀), the short, narrow brood plates with simple (vs. hook-tipped) marginal setae, deep right-angled coxal lobe of peraeopod 6, the more slender elongate dactyls of the peraeopods, and the weakly spinose uropods. Confirmation of generic assignment awaits discovery of the male of *P. chathamensis*.

Etymology

The species is known only from Chatham Island, near Victoria, B.C., in the eastern North Pacific region.

Megalorchestia Brandt 1851

Orchestoidea: Stebbing, 1906a, p. 527 (partim)
:Bulycheva, 1957, p. 130 (partim)
:Bousfield, 1957, p. 120 (partim)
:Barnard, 1969a, p. 471 (partim)

Diagnosis

Medium to large, smooth-bodied, heavily spinose substrate-modifying talitrids of the eastern North Pacific rim region, characterized by: head short, deep, inferior antennal sinus wide, shallowly incised, but deep to accommodate large segment 1 of antenna 2 peduncle; buccal mass directly ventral; eye medium to very large. Antenna 1 shorter than peduncle 4 of antenna 2, flagellum shorter than peduncle. Antenna 2 sexually dimorphic, often elongate and/or peduncle incrassate in male, peduncle 4 (♀) not shortened. Mandibular left lacinia cleanly 5–6 dentate, right lacinia tricuspate; maxilliped palp 3-segmented, "tall", segment 2 with pronounced spinose mediodistal lobe, segment 3 subconical, narrowing distally. Coxa 1 deep, anterodistal angle subacute; coxae 2–4 subquadrate, variously cuspate behind. Gnathopod 1 (♂) powerfully fossorial, spinose, carpus elongate (anterior margin nearly equal to basis) with posterodistal tumescence; propod elongate, narrowing distally, lacking true palm, postero-distal blister very shallow or lacking; gnathopod 1 (♀) segments 5 and 6 lacking blister, 6 without palm. Gnathopod 2 (♂) powerfully subchelate, palm of propod variously oblique and toothed, dactyl often with posterior marginal tooth near hinge; gnathopod 2 (♀), basis more or less strongly expanded anteromedially; segment 3 short; 4 with elongate posterior process; 5 shallow-tumescent behind; 6 shorter than 5. Peraeopods 3–7 cuspidactylate, dactyls slender; peraeopod 4, segment 5 and dactyl shorter than in peraeopod 3, dactyl constricted distally, overhanging base of unguis. Peraeopods 5–7 tending to dissimilarity (in southern species); peraeopod 6 slightly longer than peraeopod 7, all strongly spinose, dactyls moderately long. Coxa 5 anterolobate; coxa 6 posterolobate. Abdominal side plates nearly smooth behind and below, hind corners weakly acuminate, 2 deepest, lower margin convex. Pleopods strongly reduced, 3rd shortest; peduncular outer margin long-spinose, inner margin with 2 retinacula. Uropods 1 and 2, peduncles and both rami marginally strongly spinose; uropod 3 medium, short spinose; ramus longer than peduncle, laterally compressed, apex rounded. Telson short, broad, lobes nearly totally fused, with dorsal and apical short spines. Coxal gills small, longest on peraeopod 6. Brood plates subovate, lacking on peraeopods 2–4 in some species, margins with simple setae, small on peraeopod 5.

Type-species: *Megalorchestia californiana* Brandt 1851 (original designation)

Additional species: *Megalorchestia pugettensis* (Dana 1853)
Megalorchestia corniculata (Stout 1913)
Megalorchestia benedicti (Shoemaker 1930)
Megalorchestia minor (Bousfield 1957)
Megalorchestia columbiana (Bousfield 1958)
Megalorchestia dexterae new species

Remarks

The phyletic separation of heavily-bodied 4-dentate sandhoppers of the southern hemisphere from heavy-bodied 5-dentate sandhoppers of the northern hemisphere has necessitated removal of the North American Pacific complex from *Orchestoidea* Nicolet 1849 and resurrection of the genus *Megalorchestia* Brandt 1851 to accommodate them. *Megalorchestia* presently contains three distinctive sub-groups: the *californiana* group (monotypic); the *columbiana* group (3 species); and the *pugettensis* group (3 species), as diagnosed herewith (pp. 29–40, and figs. 12–18, 27). Possible formal recognition of these subgroups awaits study of more extensive material from southern California, the Gulf of California, and western Alaska.

Key to species of *Megalorchestia*

1. Eyes medium, vertically subquadrate, not bulging from head surface; antenna 2 short, flagellum distinctly shorter than peduncle, peduncular segments 4 and 5 short, stout, strongly incrassate in male; peraeopod 4, segment 5 very short, width nearly equal to length ..... *pugettensis* group 2
Eyes large, subrotund, more or less bulging from sides of head in dorsal view; antenna 2, flagellum equal to or longer than peduncle, elongate in males, peduncle moderately incrassate in males; peraeopod 4, segment 5 width about ½ to ⅔ length 4
2. Uropod 2, outer ramus distinctly shorter than inner; peraeopod 5, segments 3 and 4 very broad (3 broader than long), differing in form from those of peraeopod 6 and 7; gnathopod 2 (♂), palm with large distal tooth and deep depression near hinge ..... *M. benedicti* (Shoemaker) (p. 40)
Uropod 2, rami subequal; peraeopod 5, segments 3 and 4 not unusually broad, not markedly different in form from those of peraeopod 6 and 7; gnathopod 2 (♂) with strong palmar tooth near hinge 3
3. Coxa 5 very deep, anterior lobe as deep as coxa 4; coxa 6, hind lobe very deep, anterior margin vertical; gnathopod 2 (♂), posterodistal angle of palm rounded ..... *M. corniculata* (Stout) (p. 39)
Coxa 5, anterior lobe distinctly shallower than coxa 4; coxa 6, hind lobe with oblique anterior margin; gnathopod 2 (♂), posterodistal angle of palm with paired short protuberances between which tip of dactyl closes ..... *M. pugettensis* (Dana) (p. 37)
4. Peraeopod 5, segments 3 and 4 very broad, differing in form from those of peraeopod 6 and 7 (fig. 3f); coxa 5 shallow, anterior lobe not as deep as coxa 4; uropod 1, outer ramus with only outer marginal row of spines; gnathopod 2 (♂), palm with acute tooth near hinge, dactyl sinuous or with posterior tooth near hinge ..... *columbiana* group 5
Peraeopod 5, segments 3 and 4 normal, differing little in form from those of peraeopod 6 and 7; coxa 5, anterior lobe about as deep as coxa 4; uropod 1, outer ramus with inner and outer marginal row of spines; gnathopod 2 (♂), palmar hinge tooth broad, blunt, dactyl regular ... *M. californiana* Brandt (p. 30)
5. Peraeopod 5, dactyl very short and stout, nail (unguis) lacking; uropod 2, outer ramus with only outer marginal spine row; gnathopod 2 (♂), palm very oblique, posterior margin of propod distinctly less than half the anterior margin ..... *M. dexterae* n. sp. (p. 35)
Peraeopod 5, dactyl short but not stout, nail developed; uropod 2, outer ramus with both inner and outer marginal row of spines; gnathopod 2 (♂), palm normally oblique, posterior margin of propod about half anterior margin 6
6. Peraeopods 6 and 7 slender, elongate, segment 6 longer than 5; gnathopod 2 (♀), posterior tumescent process of segment 4 very large, deeper than segment; animals slender, small (to 15.0 mm) ..... *M. minor* (Bousfield) (p. 33)
Peraeopods 6 and 7 stout, heavy, segment 6 not longer than 5; gnathopod 2 (♀), posterior process of segment 4 short, not deeper than segment; animals heavy bodied, large (males to 22.0 mm) ..... *M. columbiana* (Bousfield) (p. 32)

Megalorchestia californiana Brandt 1851
Figure 12

Megalorchestia californiana Brandt 1851b, p. 311; Brandt 1851c, p. 142, pl. 6
Orchestoidea californiana: Stebbing, 1906a, p. 528
:Bousfield, 1957, p. 122, pl. 24; 1958, p. 891, fig. 10j; 1961, p. 11; 1975, p. 355, fig. 229
:Bowers, 1963, p. 316, figs. 1, 3a; 1975, p. 355 fig. 224

Material examined

British Columbia: E.L. Bousfield stations, 1959, Vancouver Island, outer coast, Cape Scott southward, 174 specimens from stns. O1, O2c, O3, O5, O7c, O12, O16, O18; inner coast, north end, 55 specimens from V1, V2; south end 22 specimens from Chatham Island; *ibid.* 1964, Vancouver Island, near Bamfield, 42+ specimens from H44, H45; *ibid.* 1970, P707 (Pachena Bay), Vancouver Island, 40 specimens; *ibid.* 1975, P14b, (Keeha

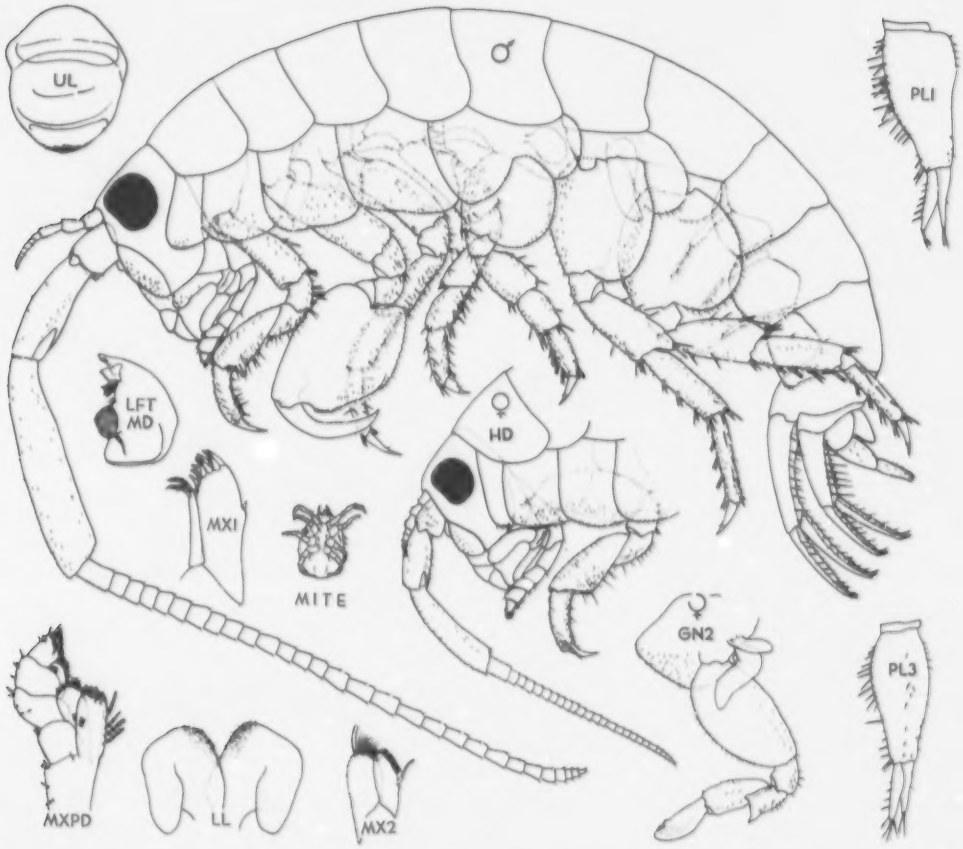

Figure 12. *Megalorchestia californiana* Brandt. Brady's Beach, Vancouver Island, B.C. ♂ - 23.0 mm, ♀ ov. - 20.0 mm.

Bay), 84 specimens; *ibid.* 1976, B6 (Brady's Beach), 3 ♂♂, 3♀♀ (fig'd specimens); *ibid.* 1977, 13 specimens from B5e (Witty's Lagoon), B11c (Wreck Bay).

Washington State, USA: Bousfield 1957 stn. M14 (Fidalgo Island), 60+ specimens; *ibid.* 1966, 120 specimens from W14, W16, W17, W20, W34, W39, W41, W45, W46, W47.

Oregon State (outer coast) *ibid.* 1966: 68 specimens from W50, W53, W55, W56, W59, W61, W63, W66, National Museum of Natural Sciences collections.

Miscellaneous collections: **British Columbia**, Vancouver Island, Young and Spreadborough collections, 1909: (1) Wreck Bay, 11 June, 7 ♂♂, 3 ♀♀ ov. (2 lots), NMNS No. 1047; Ucluelet (Long Beach), July, 9 ♂♂, 1 ♀, 8 imm. NMNS No. 5115; "Long Bay" (Ucluelet), Lot. No. 23, 20 July 1931, C.G. Carl coll., 10 ♂♂, 8 ♀♀, NMC-C-1981-570. JFL Carl collections, Vancouver Island 1934, stns. 2231-14S, May; 2241-12, 28 June, 10 imm.; Cadborough Bay, Victoria, 8 June 1956, 1 ♂, 8 ♀♀ (3 ov.) NMNS No. 5116; Sydney Spit, coarse sand at HW, 26 August 1956, 2 ♂♂ subad. NMNS No. 10348.

California: Santa Barbara, sand beach, 25 October 1965, W.L. Klawe coll., 4 ♂ subad., 1 ♀ br. I, 12 imm., NMNS No. 13974; Santa Barbara, August, 1969, A.Wenner coll., 8 ♂♂, 5 ♀♀, NMNS No. 13975. Re-examined all materials from British Columbia, California, and Bahia San Quintin, Mexico, previously recorded by the author (1957, 1961, 1964), NMNS collections.

Remarks

M. californiana is close to the apomorphic *columbiana* group in overall form of body and appendages, but differs in the larger body size, less shortened urosome, undifferentiated peraeopod 5, deeper coxal plates (especially of peraeopod 5), more spinose abdominal side plates, and more heavily long-spinose uropods 1 and 2. Also, the eyes are not as large, relative to head size, the maxilliped palp segment 2 is broader, gnathopod 1 (♀) carpus broadens distally, dactyl of gnathopod 2 (♂) is untoothed behind; the peraeopod dactyls are relatively short and stout, the gills less markedly reduced, and the mature female has fully developed brood plates on peraeopods 2 to 5. The dorsal abdominal markings are less striking than in *M. columbiana* (see Bowers, 1975), but the brilliant orange-red colour of antenna 2 of mature males is diagnostic.

Distributional ecology

Occurs only on smooth sand beaches of open coasts exposed to surf action and cool, high salinity waters; it ranges from the north end of Vancouver Island, B.C., southward to Point Conception, California, and sporadically south to northern Baja California. The species is univoltine, breeding once per year; females ovigerous in spring and early summer. Like most semi-terrestrial talitrids of Pacific rim shores, *M. californiana* is frequently parasitized on gills and sternum by mites (*Thinoseius* sp.).

Columbiana group

This highly apomorphic sandhopper group is characterized by relatively slender bodies and very short urosome; large, bulging eyes; elongate antenna 2; shallow coxal plates; slender peraeopod dactyls; markedly reduced and different form of peraeopod 5; unequal rami of uropod 2; and reduced gills and brood plates. All occur on fine to coarse sand beaches but often on protected, steeper shores, subject to brackish or even freshwater influence.

Megalorchestia columbiana (Bousfield 1958)
Figure 13

Orchestoidea columbiana Bousfield 1958, p. 890 fig. 4; 1961, p. 9, fig. 4f-h; 1975, p. 355, fig. 233 :Bowers, 1975, p. 355, fig. 226; 1963, p. 317, fig. 3d

Material examined

Alaska: 260 specimens from Bousfield & McAllister 1961 stns. A20, A22, A58, A60, A61, A65, A66, A70, A71, A73, A87, A155 (Day Harbour, near Seward, to Dixon entrance).

British Columbia: Queen Charlotte Islands, 4 specimens from Bousfield 1957 stns. H13, E1; north mainland coast; 90 specimens from E.L. Bousfield 1964 stns. H35, H38, H40, H44, H45, H48, H60; E.L. Bousfield 1959 stn. N3, 200+ specimens; Vancouver Island, north end: 19 specimens from E.L. Bousfield 1959 stns. O2a, O2c, V1; Vancouver Island, south end; 36+ specimens from E.L. Bousfield 1970 stns. P713 (Clo-oose Beach) and P720 (Port Renfrew).

Washington State: 70 specimens from E.L. Bousfield 1966 stns. W16, W20, W21, W24, W26, W38, W39, W45, W46.

Oregon State: 45 specimens from E.L. Bousfield 1966 stns. W50, W52, W56, W59, W63, W64. Re-examined all material from British Columbia and California including type material from Wickininnish Bay, and figured material from Carmel Beach, Monterey Co., California, previously published by the author (1958, 1961). NMNS collections, Ottawa.

Remarks

Megalorchestia columbiana is the most plesiomorphic member of the group in having a relatively large, stocky body; short, heavy peraeopods; and (with the closely related *M. minor*) a more vertical palm of gnathopod 2 (♂); normal dactyl of peraeopod 5; and both margins of the outer ramus of uropod 2 spinose. On surf-exposed fine sand beaches the animal occasionally co-occurs with *M. californiana* from which it is distinguished by the more conspicuous dorsal abdominal markings (at all stages) and shorter urosome, and by the bluish-white antennae of the mature male (Bowers, 1963). In northern and central regions, especially on protected coarse sand beaches, it co-occurs frequently with *M. pugettensis*; the dorsal colour patterns are often difficult to distinguish, but *M. columbiana* is usually less darkly pigmented; moreover, the body of *M. columbiana* is broader anteriorly, and the eyes appear to bulge from the head margin in dorsal view. *M. columbiana* is superficially similar to *Trinorchestia trinitatis* Derzhavin in the large eyes, elongate antenna (♂), and form of gnathopod 2 (♂), but is readily distinguished by the elongate narrowing propod

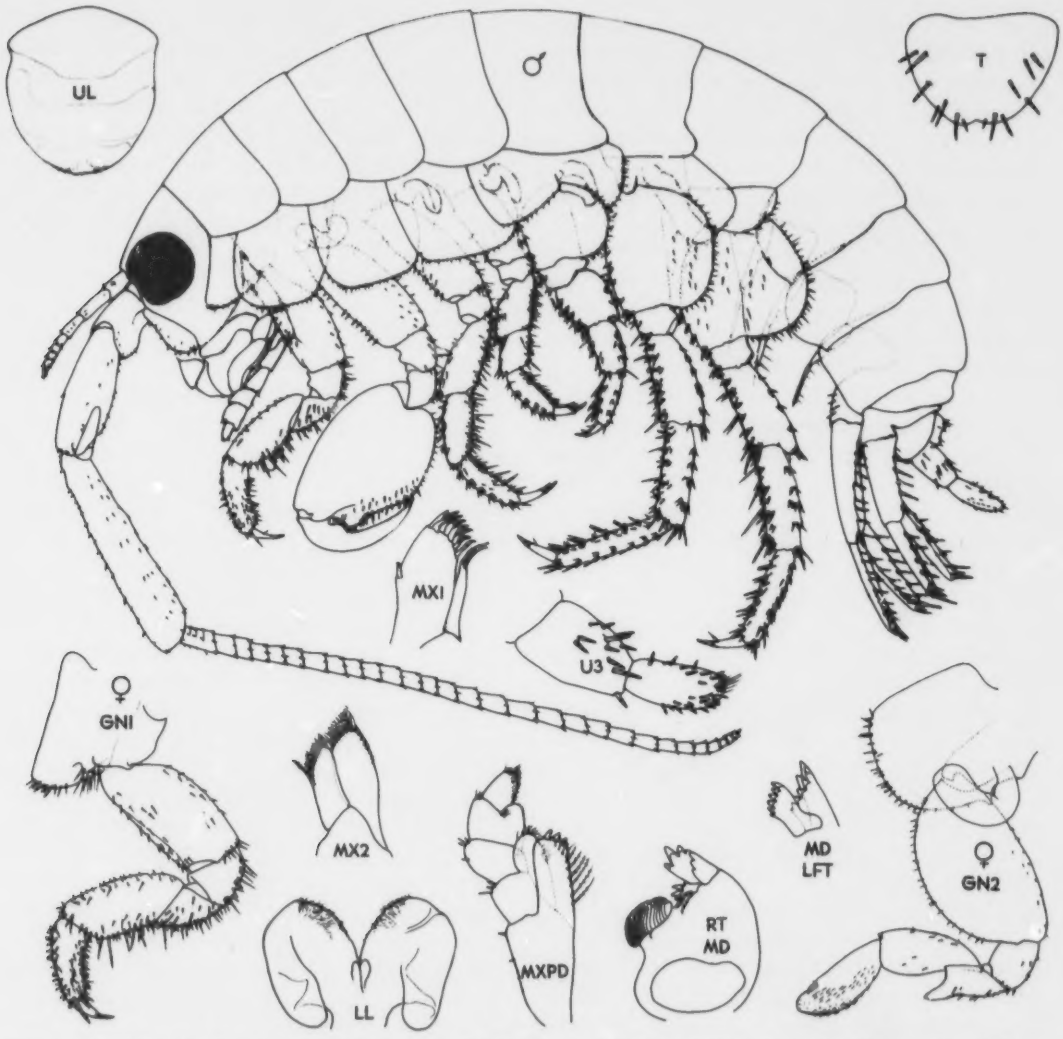

Figure 13. *Megalorchestia columbiana* (Bousfield). Carmel Point, California. ♂ - 22 mm, ♀ - 16.0 mm.

of gnathopod 1 (both sexes), the specialized constriction overhang of the dactyl of peraeopod 4, and much more reduced and modified pleopods, and the specialized form of peraeopod 5.

Distributional ecology

Occurs at the level of drift debris and slightly below, mainly on protected, steeper-sloping, fine-to-coarse sand beaches of estuaries and embayments, often in brackish areas, from southern Alaska (northern and western limit not determined) to Carmel Point, Monterey Bay, central California. The species is univoltine, breeding once per year, females ovigerous in the spring and early summer. Animals occur on the same beaches as, but slightly seaward of, *M. californiana*, burrow not quite as deeply, and tend to be more diurnal (especially the juveniles and immatures).

Megalorchestia minor (Bousfield 1957)
Figure 14

Orchestoidea minor Bousfield 1957, p. 126, fig. 25
:Straughan, 1981, p. 375
Orchestoidea columbiana: Straughan, 1981, p. 375

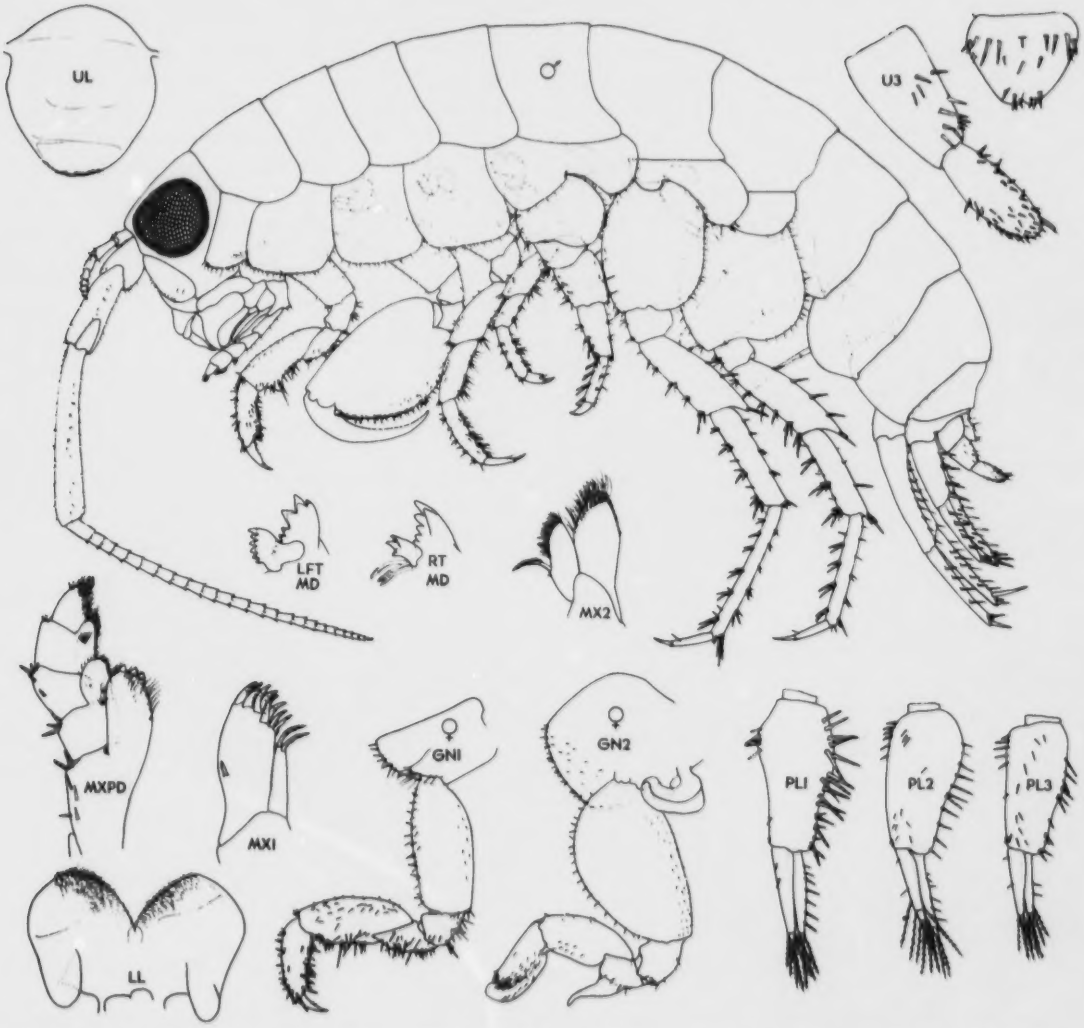

Figure 14. *Megalorchestia minor* (Bousfield). Pt. Dume, California. ♂ - 14.0 mm, ♀ ov. - 15.0 mm.

Material examined

California: D.E. Bowers collections, April 1960 from: San Simeon, San Luis Obispo Co., 9 ♂♂ (to 14.0 mm), 9 ♀♀, 5 imm., NMNS No. 5430; Santa Barbara, Santa Barbara Co., 16 ♂♂, 16 ♀♀, br. P5 only, NMNS No. 5431; west side, Pt. Magu, Ventura Co., 3 ♂♂, 2 ♀♀, NMNS No. 5428; between Pt. Magu and Sycamore beach, 11 ♂♂, 28 ♀♀, NMNS No. 5435; just east Seguit Pt., Los Angeles Co., 7 ♀♀, NMNS No. 5427; Dume Cove, Los Angeles Co., 7 ♀♀, NMNS No. 5433; just west Pt. Dume, Los Angeles Co., 14 ♂♂, 17 ♀♀, NMNS No. 5432; Municipal Beach, Los Angeles Co., 4 ♂♂, 14 ♀♀, NMNS No. 5434. Santa Barbara, Santa Barbara Co., sand beach at HW Level, 25 October 1965, W.L. Klawe coll., 3 ♂♂, subad., 4 ♀♀ br. P5 (to 14.5 mm), 2 imm. NMC-C-1981-503, slide mounts; *ibid.* August 1969, A. Wenner coll., 3 ♀♀ br. P1, P5 only (to 11.0 mm), NMC-C-1981-505.

Mexico: Bahia San Quintin, HW stn. SQ104, 5 August 1960, J.L. Barnard coll., 1 (peraeopod 6 only)?. Re-examination of all specimens from California (Playa del Ray, Pt. Dume) and Mexico (Ensenada, B.C.), including type slide

mounts (basis of fig. 14), reported in previous author publications (1957, 1961).

Distributional ecology
Occurs on surf-exposed flat sand beaches, burrowing at or near the HW drift debris, from just north of Pt. Conception (San Luis Obispo Co.) to northern Baja California (Ensenada and Bahia San Quintin). The species is probably univoltine; ovigerous females have setose brood plate only on peraeopod 5.

Remarks
The species has been seldom collected and little studied since the original description based on material from Los Angeles county, California (Bousfield, 1957). The species is small and slender-bodied (mature males to about 15.0 mm), and is distinguished from the closely related *M. columbiana* by the relatively shorter antenna 1; more slender and less heavily spinose peraeopods and uropods; more markedly modified peraeopod 5 (nail of dactyl shorter); less strongly developed hinge tooth of palm and dactyl of gnathopod 2 (♂); more elongate posterior process of segment 4 of gnathopod 2 (♀); and the more spinose armature of the outer ramus of uropod 2 which (in *M. minor*) extends further apically along the inner margin than along the outer margin. The species occurs mainly on beaches that are exposed to relatively heavy contamination from offshore oil wells and urban pollution in the southern California region (e.g. Straughan, 1981) and might be considered an endangered crustacean species.

Megalorchestia dexterae new species
Figure 15

Material examined
San Juanico, Baja California, sand beach at HW level, 21 July 1975, D.M. Dexter, coll. Male holotype (17.0 mm), female allotype (br. I., 13.5 mm), male subadult paratype (11 mm). NMC-C-1981-506, slide mounts.

Diagnosis
Male (17.0 mm). A medium-sized, slender-bodied, finely spinose species of the *columbiana* group characterized by: eyes very large, nearly contiguous dorsally, and posteriorly nearly reaching peraeon 1; antenna 1, flagellum 5–6 segmented; antenna 2, peduncle long, segment 4 long; flagellum about 25-segmented, subterminal segments weakly toothed. Maxilliped palp relatively short, segment 3 short. Gnathopod 1, propod long, slender, arcuate, nearly equal in length to carpus, without posterodistal tumescence; carpus very elongate, with small posterodistal blister. Gnathopod 2, propod large, ovate, palm very oblique, stoutly spinose, especially at posterior angle, with large rounded tooth near hinge; posterior margin short, about one-quarter anterior margin; dactyl long, sinuous. Peraeopods 3–7, dactyls relatively slender, dactyl of 4 not strongly pinched, barely overhanging base of nail; peraeopod 5, anterior marginal peg-spines of segment 6 short; dactyl very short, thick, not "fuzzy" behind, apex blunt, nail lacking; peraeopods 6 and 7 slender, elongate, bases subsimilar in shape, segment 6 about equal to 5. Abdominal side plates very weakly setulose behind, smooth below. Pleopods 1–3, rami very short, 1–2 segmented, scarcely half length of respective peduncles. Uropods 1 and 2, peduncles and rami slender, armed with numerous relatively long slender simple spines; outer ramus of uropod 2 distinctly shorter than inner ramus, with outer marginal spines only. Uropod 3 relatively long, not markedly sexually dimorphic, ramus about equal in length to peduncle. Telson short, small, apex subacute, entire, dorsal spines slender.

Female (13.5 mm., br. I). Antenna 2, flagellum as long as peduncle, about 25-segmented, subterminal segments toothed behind. Gnathopod 2, basis broadest medioproximally; hind lobe of segment 4 short, not deeper than segment, segment 5 hind lobe with small distal process. Brood plates not developed in single specimen available.

Etymology
The species is named in honour of Dr. Deborah M. Dexter, the collector, who has specialized in the world-wide study of sand-beach crustaceans.

Distributional ecology
Known only from the type locality which is the most southerly record of the genus (sens. str.) on the North American Pacific coast.

Remarks
Megalorchestia dexterae bears a superficial resemblance to some members of *Pseudorches-*

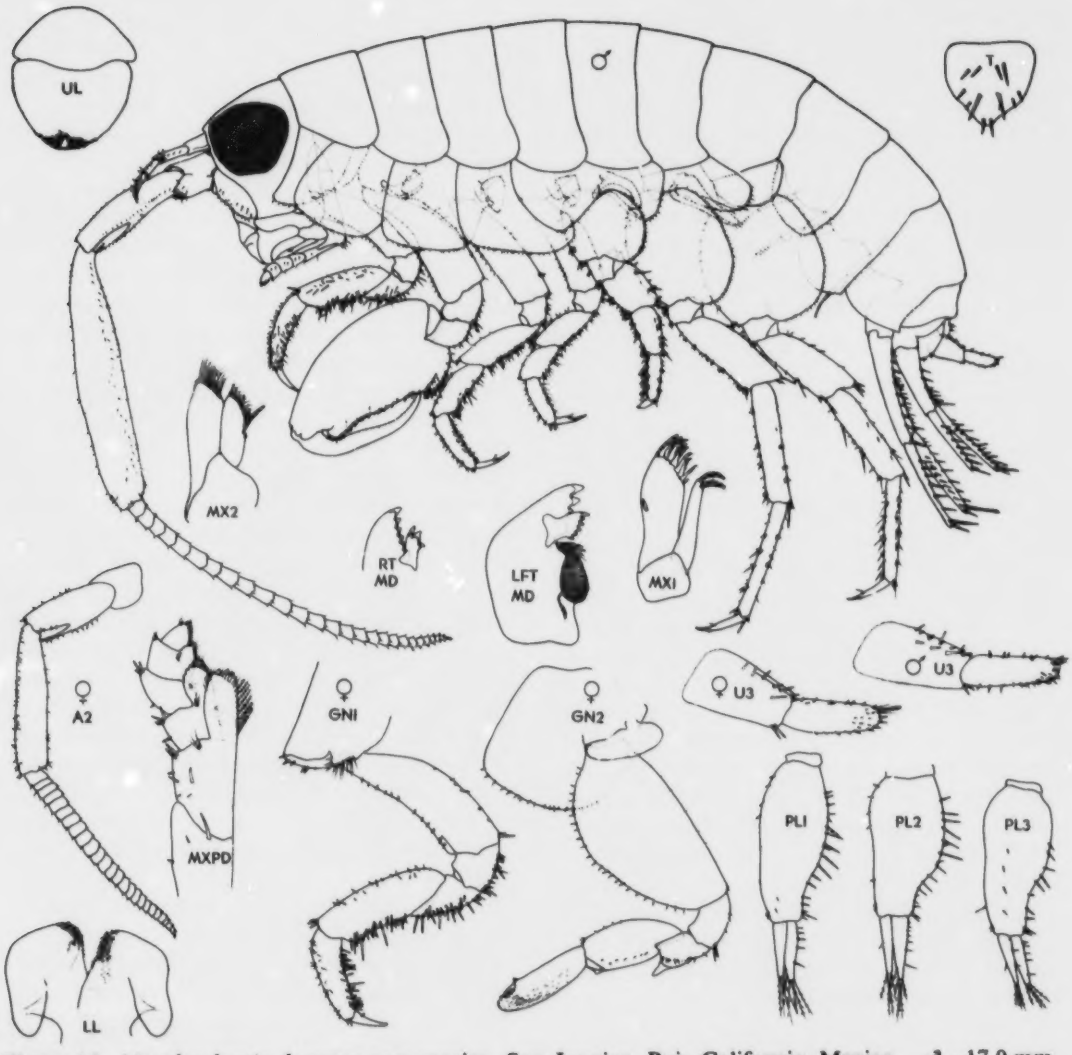

Figure 15. *Megalorchestia dexterae* new species. San Juanico, Baja California, Mexico. ♂ - 17.0 mm, ♀ br. I. - 13.5 mm.

toidea, especially *P. gracilis* Bousfield & Klawe, with which it may abut distributionally in Baja California. These similarities include the relatively slender body, large eyes, elongate antenna 1, relatively shallow coxal plates, form of gnathopod 2 (♂), distinctive peraeopod 5 (especially dactyl), and slender uropods. The generic differences, however, include in *Megalorchestia* a less elongate body, slightly incrassate peduncular segments of antenna 2 (♂), taller maxilliped palp, more elongate and more powerfully fossorial gnathopod 1, smaller coxal gills, and differing form of the pleopods, uropod 3 and telson.

Pugettensis group

This relatively plesiomorphic complex is characterized by a short, broad, stocky body; relatively small eyes; short antennae with stoutly incrassate peduncular segments (♂); deep coxal plates, especially the lobes of peraeopods 5 and 6;

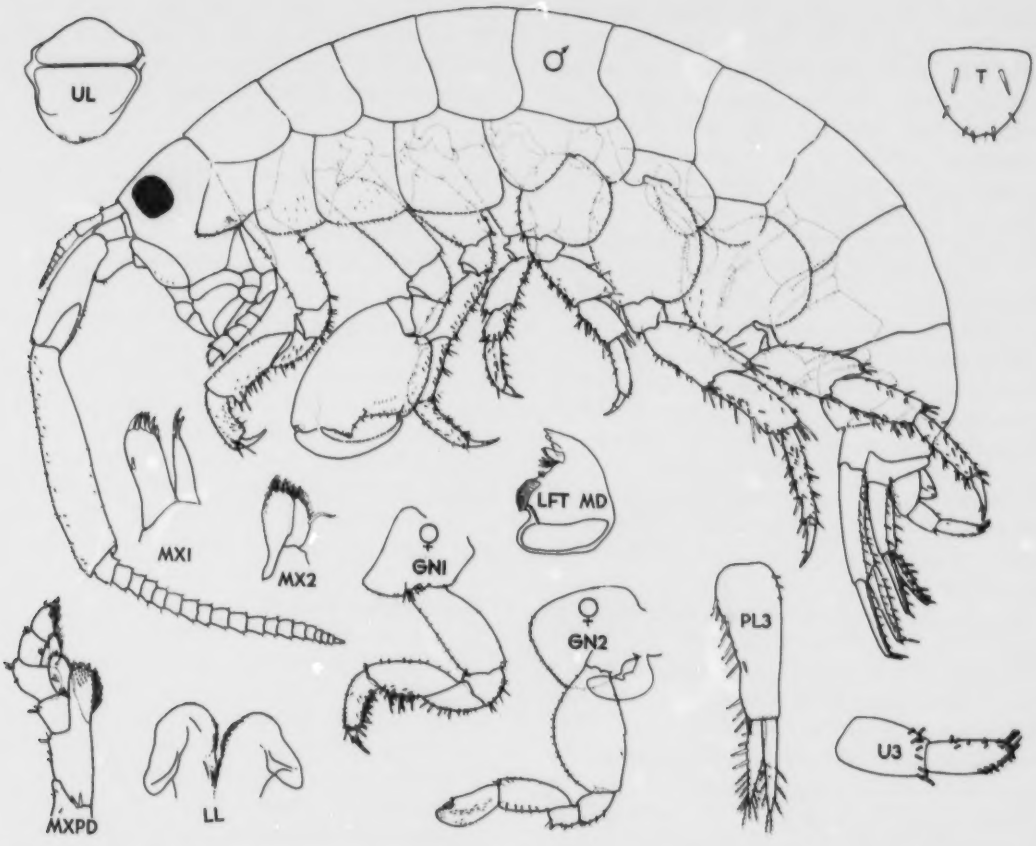

Figure 16. *Megalorchestia pugettensis* (Dana). Brady's Beach, Vancouver Island, B.C. ♂ - 17.0 mm, ♀ - 13.5 mm.

strongly toothed, normally oblique palmar margins of gnathopod 2 (♂), dactyl not toothed behind; relatively short, stocky, short-dactylate peraeopods; subsimilar form of peraeopods 5–7; segment 4 very short in peraeopod 4; and short uropods and telson. The two larger species occur more frequently on coarse sand and fine gravel, often on protected shores, whereas the smaller *M. benedicti* is an open surf, fine sand beach dweller.

Megalorchestia pugettensis (Dana 1853–55)
Figure 16

Orchestia (*Talitrus*) *pugettensis* Dana 1853 and 1855 p. 859, t. 57, fig. 3a-d
Orchestoidea pugettensis:Stebbing, 1906a, p. 528
:Thorsteinson, 1941, pl. 1, figs. 1-9
:Bousfield, 1958, p. 890, fig. 10i; 1961, p. 7, fig. 3; 1981, fig. 18; 1975, p. 355, fig. 232
:Bowers, 1963, p. 317, figs. 3e, 4; 1975, p. 357, fig. 228
:Staude *et al.*, 1977, p. 12, fig. 20a
Orchestoidea corniculata: Thorsteinson, 1941, p. 55
Talorchestia tridentata: Stebbing, 1899, p. 398, t. 30b (male)

Material examined
Alaska: 290 specimens from Bousfield and McAllister 1961 stns. A22, A43, A61, A66, A68, A70, A127, A140 (Prince William Sound to Baranof Is.).
British Columbia: Queen Charlotte Islands; 260+ specimens from Bousfield 1975 stns. W1, W9a, W11, W16, H13, E18b, E20; north main-

land coast; 270 specimens from Bousfield 1964 stns. H1, H2, H4, H11, H20, H23, H34, H35, H38, H40, H42, H44, H48, H51, H60; central mainland coast, 445+ specimens from Bousfield 1959 stns. N1, N3, N4, N6, N11, N16, N22; Vancouver Island, north outer coast, 715+ specimens from Bousfield 1959 stns. O1, O2c, O3, O5, O7, O12, O16, O18, 58 specimens from Bousfield 1975 stns. P23, P29; north inner coast and Johnstone Strait, 545+ specimens from Bousfield 1959 stns. V1, V2, V3, V4b, V22; Strait of Georgia: re-examination of Bousfield 1955 station material from G1, G4, G9, G13, M1, M8, M11; southern Vancouver Island, 190 specimens from Bousfield 1970 stns. P710, P714, P716, P717, P720, and 5 specimens from Bousfield 1975 stns. P6, P14 (Barkley Sound region).

Washington State: 145 specimens from Bousfield 1966 stns. W2, W4, W8, W24, W26, W30, W31, W33, W35, W36, W38, W41, W42, W44, W47, W48.

Oregon coast: 50 specimens from Bousfield 1966 stns. W53, W55, W56, W58, W60.

California: Re-examination of material of Bowers and author from Monterey region, previously published by Bousfield (1961).

Miscellaneous material: **British Columbia**, Vancouver Island region: Ucluelet, July 1909, J. Macoun coll., 18 ♂♂ (to 16.0 mm), 3 ♀♀, 1 imm. NMNS No. 913; J.F.L. Carl collections: head Departure Bay, 28 July 1938, 1 ♂, 1 ♀, 2 imm., Cabbage Is., Strait of Georgia, 30 August 1956, 11 ♂♂, 18 ♀♀, NMNS No. 5109; Gonzales Bay, 27 February 1956, 3 ♀♀, 4 imm., NMNS No. 5108; Cadboro Bay, 25 February 1956, 2 ♂♂, 3 ♀♀, 1 imm. NMNS 5107; *ibid.*, 8 June, 5 ♂♂, 2 ♀♀, NMNS No. 5116; *ibid.*, 15 September, 6 ♀♀ subad., (with sternal mites); Saanich Spit, 21 August 1956 (in company with *M. californiana*), 2 ♂♂, 2 ♀♀, NMNS No. 5110; China Beach, 4 July 1959, 22 ♂♂ (to 17.5 mm), 26 ♀♀, NMNS No. 5877; Chatham Island (near Victoria), 12 July 1959, 1 ♂, 3 ♀♀, NMNS No. 5869.

Diagnosis

Megalorchestia pugettensis varies in size (mature males 13.0 to 16.0 mm) and somewhat in morphology. Southernmost populations tend to have less spinose abdominal side plates, and in gnathopod 2 (♂), the posterodistal palmar process is very short or lacking, almost as in *M. corniculata*. However, the dark lateral bars on coxae 5–7, are distinctive at all pigmentation intensities throughout the range (Bowers, 1963).

Remarks

Megalorchestia pugettensis is the most plesiomorphic known species of the genus, particularly in the small eyes, relatively short propod of gnathopod 1 that (in ♂) is postero-distally tumescent (forming a "pseudopalm"), the relatively weakly and short-spinose uropods, weakly armed telson, and least broadly expanded pleopod peduncles. These characters are more or less shared with two similar-sized but more plesiomorphic western Pacific sandhoppers, *Talorchestia sinensis* Tattersall and *T. nipponensis* Morino and to a lesser extent with western Pacific sandhoppers of the even more plesiomorphic genus *Platorchestia* (see Table III, and fig. 27).

Distributional ecology

Occurs on nearly all coarse to fine sand beaches of both surf-exposed shores and protected embayments, including estuaries, washed by summer-cold to warm, high salinity to brackish waters, from southern Alaska (western and northern limits not determined) to central California (Carmel Point). *M. pugettensis* co-exists with *M. californiana* on open fine sand beaches, burrowing mainly slightly seaward of it at the drift debris (HW) level, and co-occurs frequently with *M. columbiana* at or slightly above it, under drift debris. *M. pugettensis* is the only sandhopper occurring on poorly sorted or very coarse sands of small, steeply sloping beaches, frequently with *Traskorchestia traskiana* in such wave-protected situations. *Megalorchestia pugettensis* (and possibly also *M. columbiana*) almost certainly occurs on the Alaskan peninsula and adjacent Fox Islands, probably westward at least to Unalaska (*Orchestoidea* of Sheffer 1959, p. 377). Murie (1959, p. 290) states that "sand fleas were present in unbelievable numbers under boulders and in rotting kelp on Unimak Island, where they composed almost the entire droppings of red foxes (*Vulpes vulpes* L.)." The species is univoltine, breeding once per year; females ovigerous in late winter and early spring, adults dying out during the summer.

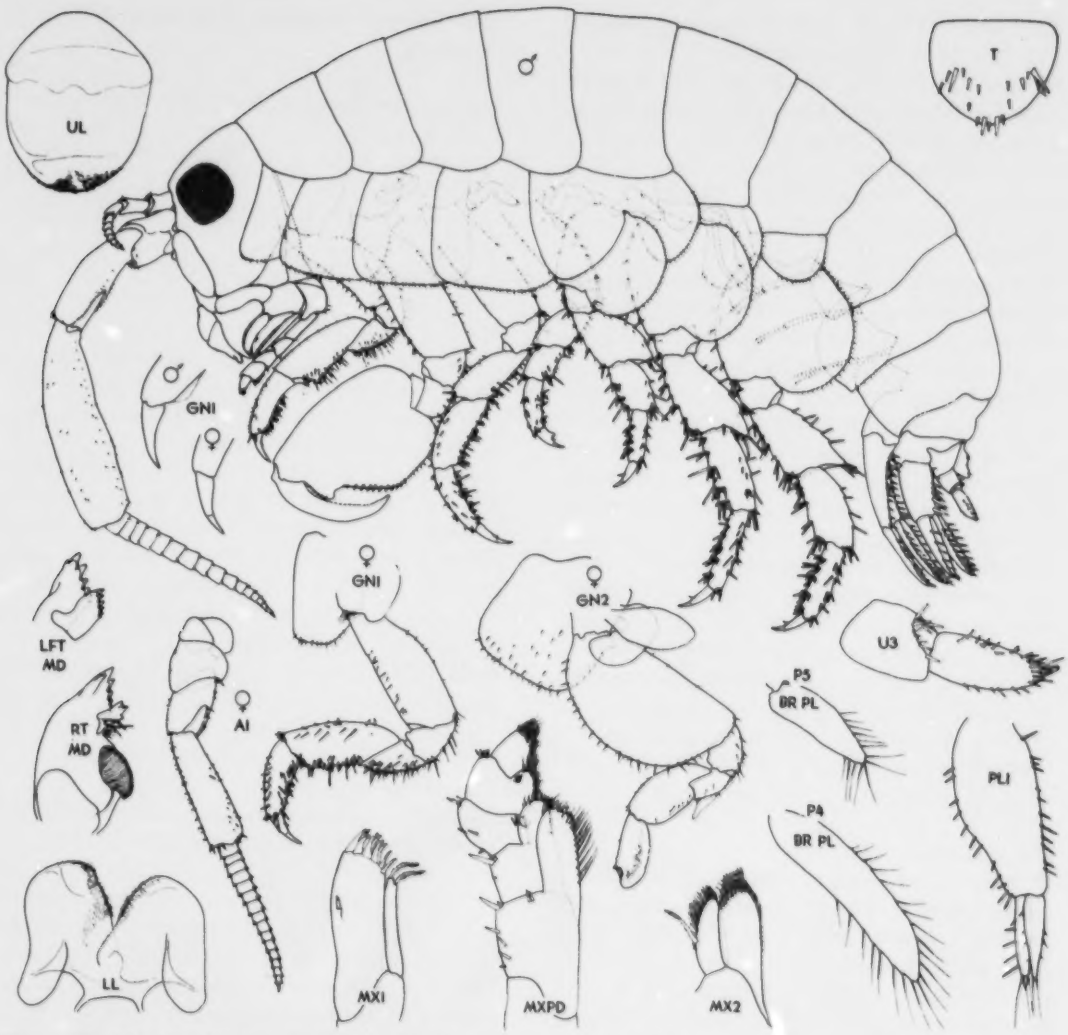

Figure 17. *Megalorchestia corniculata* (Stout). Shell Beach, California. ♂ - 21.0 mm, ♀ ov. - 18.0 mm.

Megalorchestia corniculata (Stout 1913)
Figure 17

Orchestoidea corniculata Stout 1913, p. 647, fig. C
:Bousfield, 1961, p. 7, fig. 4a-d; 1981, fig. 17
:Craig, 1973a, b.
:Bowers, 1963, p. 317, fig. 2, 5-d; 1975, p. 356, fig. 3d.
:Straughan, 1981, pp. 375, 426.
non *Orchestoidea corniculata*: Thorsteinson, 1941, p. 55

Material examined

California: Duxbury Reef, Salinas beach, 28 August 1960. B. Neal coll., 24 specimens NMC-C-1981-474; Santa Barbara Beach at HW, 14 June 1961, McGrath coll., 24+ specimens, *ibid.*, 26 June, 11 ♂♂ (to 26.0 mm); *ibid.*, 18 August, A. Wenner coll., 3 ♂♂, 4 ♀♀, 3 imm.; Corona del Mar, 28 May 1953, J.L. Barnard coll., 5 specimens, NMNS Cat. No. 5128; Pt. Loma, San Diego, February 1956, W.L. Klawe coll., 5 imm. NMC-C-1981-466. Re-examination of all central Californian material listed in Bousfield (1961, p. 7), including stn. C8,

Shell Beach, 10 July 1959, 37 specimens NMNS Cat. No. 5819, and slide mounts.
Mexico: El Socorro Beach near El Rosario, Baja California, fine sand and cobbles, under wave cast *Phyllospadix* at HHW level, June 1980, R.G. Appy coll., 10 ♂♂ (to 19.0 mm), 22 ♀♀ (mostly ov.), 10 imm. NMC-C-1981-463.

Remarks
Megalorchestia corniculata is the largest and most spinose species of the *pugettensis* group (mature males to 25.0 mm), but is otherwise very similar to *M. pugettensis*. The species is distinguished by relatively large eyes, especially in southern populations; weakly tumescent gnathopod 1 (♂); non-protruding paired spinous ridges at the posterior palmar angle of gnathopod 2 (♂); very broadly expanded basis of gnathopod 2 and small brood plate (♀); very deep anterior and posterior lobes of coxae 5 and 6 respectively; relatively short and powerfully spinose uropods; more broadly expanded pleopod peduncles; and more dorsally spinose telson. Dorsally, the pigmentation pattern is similar to that of *M. pugettensis*, but laterally, *M. corniculata* lacks a dark horizontal bar on peraeon and/or coxa 7. Antenna 2 (mature male) is usually salmon-pink, rarely bluish or brownish, as in *M. pugettensis*.

Distributional ecology
Occurs mainly on surf-exposed, high salinity, cold-temperate, coarse sand and fine gravel beaches, beneath cliffs of the California coast, from north central region (Mission Head) to northern Baja California (El Socorro Beach). Animals burrow at HW level in the zone of rotting kelp, above freshly deposited kelp, females with eggs seaward of those with young, but above most juveniles. The burrows of adults (especially females with eggs and especially in the winter) may reach depths of 50–60 cm (maximum 76 cm). Adults are exclusively nocturnal but juveniles emerge earlier in the evening and remain at the surface later in the morning, after sunrise (Craig, 1973b). The species tends to orient landwards under a wide range of stimuli by day; lunar position is the dominant night-time orienting stimulus (Enright, 1961). The species occasionally co-occurs with *M. pugettensis* in the northern part of its range, and with *Paciforchestia klawei* and *Traskorchestia traskiana* in the south, but rarely with other sandhoppers (e.g. Straughan, 1981).

Megalorchestia benedicti (Shoemaker 1930)
Figure 18

Orchestoidea benedicti Shoemaker 1930, p. 112, fig. 3
:Bousfield, 1961, p. 9; 1975, p. 355, 363; 1981, p. 86, fig. 17
:Bowers, 1963, p. 318, fig. 3c; 1975, p. 357, fig. 227
:Straughan, 1981, pp. 375, 423

Material examined
California: Piedras Blancas, San Luis Obispo Co., sand beach at HW level, 30 April 1947, J.L. Barnard coll., 1 ♀, br. pl. P5 only (8.0 mm); Santa Barbara, Santa Barbara Co., sand beach, intertidal, 25 October 1965, W.L. Klawe coll., 2 ♂♂, 1 ♀ (br. pl. P5 only), NMC-C-1981-530; Santa Barbara, sand beach, HW level, 18 August 1969, A. Wenner coll. 5 ♂♂ (to 10.0 mm), NMC-C-1981-529. All specimens from slide mounts, previously published upon from California (1957, 1961) and Mexico (Ensenada, 1957; Bahia San Quintin, 1964) were re-examined; fig. 18 is based on material from Morro Beach, San Luis Obispo Co.

Remarks
This is the smallest and most apomorphic species of the *pugettensis* complex. It differs from the other species not only in smaller size and more strongly contrasting checkerboard pigmentation pattern, but also in the more elongate propod and the deeper proximal palmar incision of gnathopod 2 (♂); the relatively narrow basis of gnathopod 2 (♀); the somewhat unlike form of peraeopod 5 (with respect to peraeopods 6 and 7); the more elongate and slender peraeopods 6 and 7, especially dactyls; the more expanded pleopod bases and shorter rami; the unequal rami of uropod 2; and the shorter, broader telson. In these features, *M. benedicti* links the *pugettensis* group with the *columbiana* group.

Distributional ecology
Occurs mainly on surf-exposed, fine sand, berm beaches from northern California (Eureka) to central Baja California. The species burrows shallowly under drift debris at HW level, just below the main population of *M. californiana* with which it frequently co-occurs.

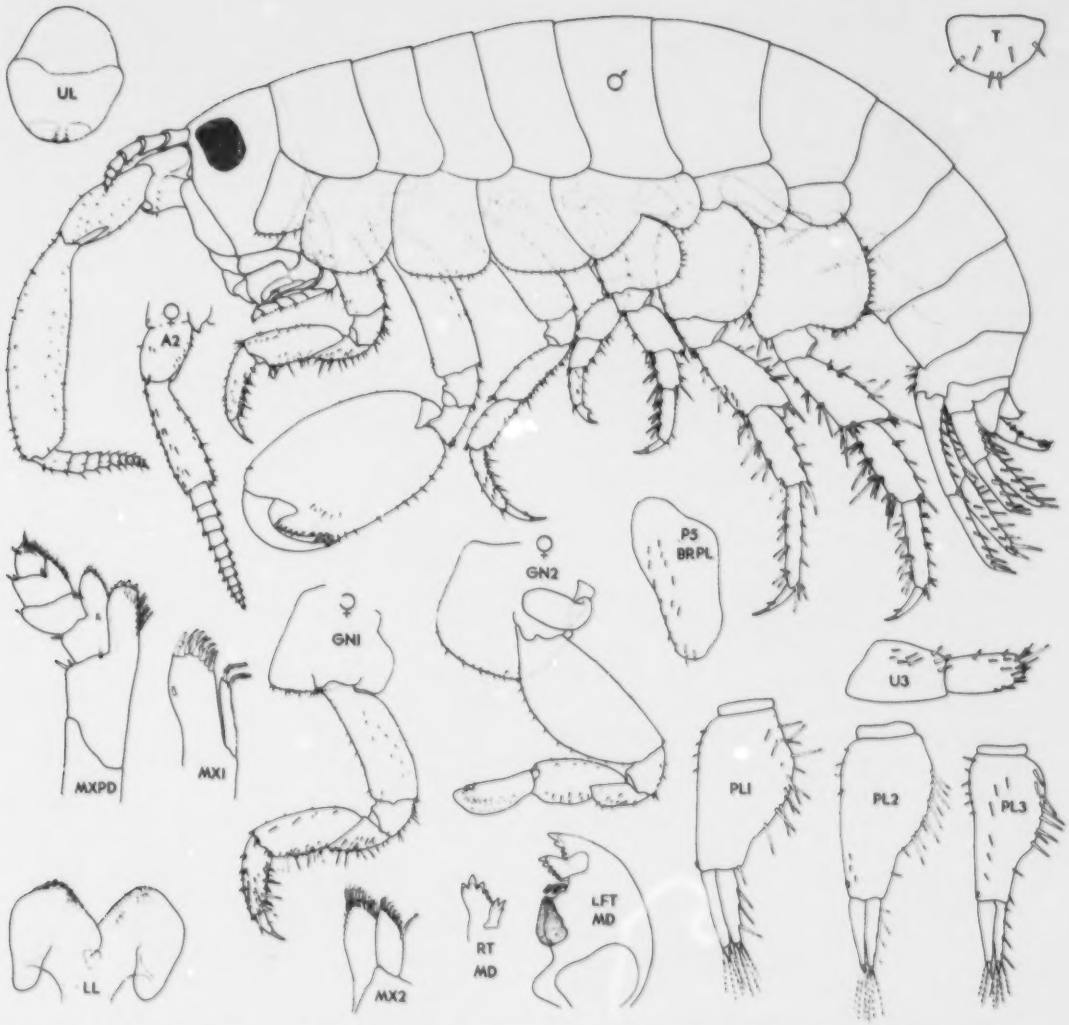

Figure 18. *Megalorchestia benedicti* (Shoem.). Morro Beach, California. ♂ - 9.5 mm, ♀ ov. - 8.0 mm.

Trinorchestia new genus

Orchestoidea: Bulycheva, 1957, p. 130 (partim)

Diagnosis

Medium-sized, slender-legged, spinose beachhoppers characterized by: body smooth, broad, narrowing abdominally; eyes very large (especially in ♂), nearly contiguous dorsally. Inferior antennal sinus medium deep, short. Antenna 1 short, peduncle 2 longest, flagellum shorter than peduncle. Antenna 2 elongate, peduncular segments moderately incrassate (♂). Buccal mass relatively shallow, directly ventral to head; mandible left lacinia cleanly 5-dentate, right lacinia tricuspate; maxilliped palp tall, segment 3 subconical, 4 fused to 3. Coxal plate 1 deep, anterodistal angle acute; coxae 2–4 subquadrate, cuspate posteriorly. Gnathopod 1, carpus elongate, powerful, propod much shorter, broadest medially, spinose, lacking palm; dactyl strong; carpus and propod with posterior tumescent lobe in male only. Gnathopod 2 (♂) powerfully subchelate; palm with notch and tooth near hinge, dactyl strong, with posterior tooth near hinge; segment 4 with posterior tumescent process.

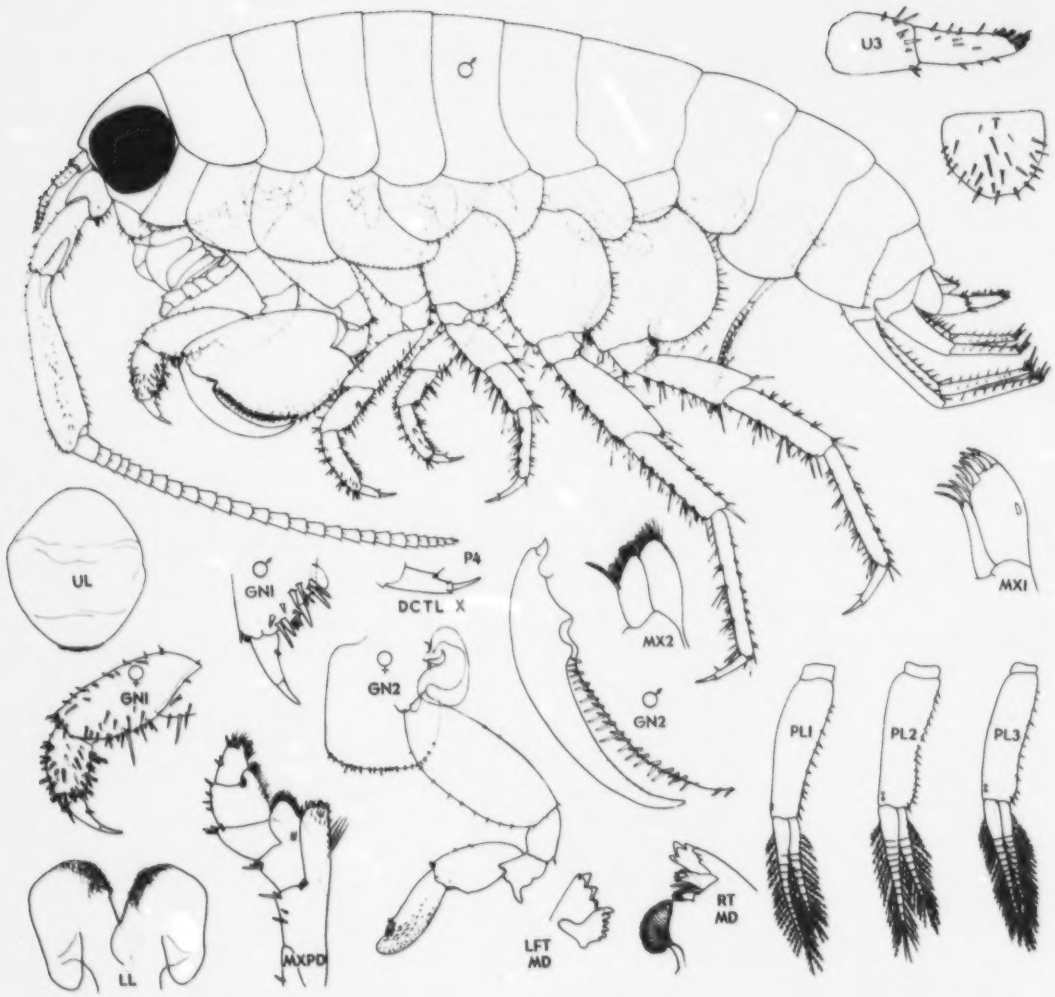

Figure 19. *Trinorchestia trinitatis* (Derzh.) Seto, Japan. ♂ - 18.0 mm, ♀ br. II. - 18.0 mm.

Gnathopod 2 (♀) basis moderately expanded anteriorly; segment 4 with posterior tumescent process. Peraeopods 3–7 slender, cuspidactylate; peraeopod 4 slightly smaller than 5, segment 4 smaller, dactyl pinched, body not overhanging base of nail; coxa 5 aequilobate, coxa 6 posterolobate, anterior margin of hind lobe convex, oblique; peraeopods 5–7 homopodous in form, basis and segment 4 similar, peraeopods 6 and 7 much longer than 5, 6 longest. Abdominal side plates smooth and convex below. Pleopods subequal, nearly normal, rami little reduced, outer ramus the shorter; peduncles sublinear, outer margins short-spinose. Uropods 1 and 2, all rami with inner and outer marginal spines, those of uropod 2 subequal in length, terminal spines simple. Uropod 3, ramus longer than peduncle, short-spinose, laterally compressed. Telson short, lobes fused distally, with dorsal and apical spines. Coxal gills 2–5 short, sinuous, 6 elongate. Brood plates undescribed.

Remarks

This monotypic genus has no single distinctive characteristic and appears not closely related to other sandhopper genera. However, shared

synapomorphies appear to relate it to *Pseudorchestoidea*, *Talorchestia*, and possibly *Megalorchestia* on the one hand (figs. 27, 28) and with the western Pacific "Talorchestia" *sinensis-nipponensis* group on the other (see Morino, 1972). The possibility that more than one species of *Trinorchestia* occurs in the western Pacific region merits careful study.

Type-species: *Orchestoidea trinitatis* Derzhavin 1937 (monotypic)

Etymology

The generic name is a combining form of *Orchestia* and the type species name *trinitatis*. Gender: Feminine.

Trinorchestia trinitatis (Derzhavin 1937)
Figure 19

Orchestoidea trinitatis Derzhavin 1937, p. 88, fig. 1
:Vader, 1970, p. 134, fig. 49
:Morino, 1972, p. 57, figs. 9–11
:Bousfield, 1981, fig. 17
Orchestoidea brito: Bulycheva, 1957, p. 134, fig. 49
Talorchestia brito: Iwasa, 1939, p. 273, figs. 13–15
:Stephensen, 1944, p. 65, figs. 22–23
:Gurjanova, 1951, p. 809, fig. 563

Material examined

Japan: Seto, Honsu, sand beach, 1957, A. Yamazi coll., 1 ♂ (18.0 mm), NMC-C-1981-536, slide mount; Ishikari, Hokkaido, 21 August 1968, H. Morino coll., 1 ♂ (18.0 mm), 1 ♂ (transforming stage), 2 ♀ ♀ (subadult, 12.5 mm), NMC-C-1981-537, slide mounts.

Distributional ecology

Occurs mainly on surf-exposed cold-temperate fine sand beaches of the open western Pacific coast from Commander Islands, Kamchatka Peninsula (including Bering and Myedny Islands) in the north, through the Kuriles, Sakhalin and Hokkaido to southern Kyushu (Japan). Life cycle is presumed univoltine, females probably ovigerous in late spring and summer. Animals are essentially nocturnal, occasionally diurnal according to availability of food (caprellids, large flies) (Morino, 1972).

Remarks

The animals are somewhat variable morphologically by region as well as sex and instar. Stephensen (1944) first drew attention to the presumed cuspidactylate condition of the peraeopods.

Orchestoidea Nicolet 1849

Orchestoidea Nicolet 1849, p. 229
:Stebbing, 1906a, p. 527 (partim)
:Barnard, 1969a, p. 471 (partim)

Diagnosis

Large, stout bodied, sculptured, strongly fossorial sandhoppers of the Pacific coast of South America, characterized by: head deflexed slightly near frons. Inferior antennal sinus shallowly incised, but deep to accommodate large peduncular segment 1. Eyes large, bulging, not contiguous dorsally. Antenna 1 short, flagellum short, peduncular segments 1 and 2 longest; antenna 2 medium, elongate, not incrassate in ♂. Buccal mass relatively shallow, directly beneath head; mandibular left lacinia cleanly 4-dentate, right lacinia tricuspate (?); maxilliped palp 3-segmented, "tall", segment 2 with spinose medio-distal lobe, segment 3 elongate, subconical, segment 4 totally lacking. Coxal plate 1 deep, anterodistal angle subacute; coxal plates 2–4 deep, hind marginal cusps vestigial or lacking. Gnathopod 1 powerful, spinose; segment 5 elongate; segment 6 elongate, narrowing distally, lacking palm; dactyl strong; segments 4 and 5 devoid of tumescent process (♂ and ♀). Gnathopod 2 (♂) powerfully subchelate, palm incised near hinge; dactyl strong, with posterior marginal swelling near hinge; gnathopod 2 (♀), basis long, little expanded, anterior margin sinuous; segment 3 short; 4 spinose behind, lacking posterior tumescent process; 5 shallow posteriorly; 6 nearly equal to 5. Peraeopods 3–7 stout, spinose, cuspidactylate, dactyls slender; peraeopod 4 shorter than 3, segment 5 distinctly shorter; dactyl pinched, body not overhanging nail. Coxa 5 aequilobate, 6 very deeply posterolobate, anterior margin vertical, rounding; peraeopods 5–7 weakly heteropodous, basis and segment 4 sub-similar in form, 6 and 7 much longer than 5, 6 longest. Abdominal side plates 1–3 deep, convex and smooth below, hind margins spinose; pleopods reduced, decreasing posteriorly, rami shorter than peduncle; peduncles broadly sublinear, outer margin strongly long-spinose, overhanging outer ramus, inner margin with 2 retinacula. Uropods 1 and 2 stout; peduncles and rami, inner and outer margins strongly spinose, terminal spines simple; rami of uropod 2 sub-

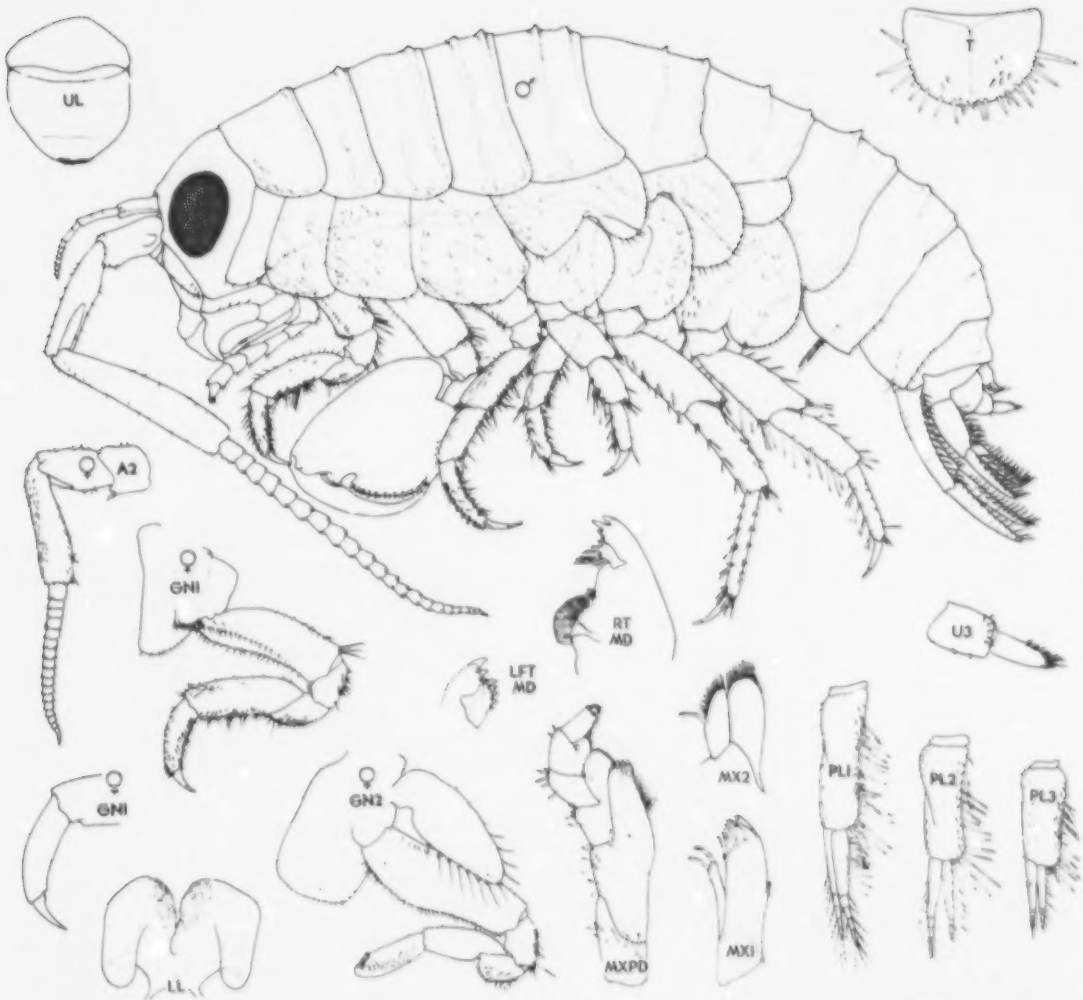

Figure 20. *Orchestoidea tuberculata* Nicolet. Chachagua, Chile. ♂ - 21.0 mm, ♀ br. II. - 17.0 mm.

equal in length. Uropod 3 very short, peduncle not expanded, short-spinose; ramus compressed, rounding apically, short spinose. Telson short, broad, lobes fused distally to form a single plate, with marginal and apical spines only. Coxal gills not greatly reduced, shallow-acetabulate, 2 and 6 longest. Brood plates subovate, subequal on 2–5, marginal setae simple.

Type-species: *Orchestoidea tuberculata* Nicolet 1949 (monotypic)

Remarks

The diagnosis (above) is based on the type-species which has never been fully described. The genus belongs to a southern hemisphere group of sandhoppers in which the mandibular left lacinia is primarily 4-dentate, the frons is slightly deflexed; antenna 2 (♀), especially peduncular segment 4, very short; coxal plates deep; hind lobe of coxa 6 very deep, anterior margin vertical; gnathopod 2 (♀), basis narrow, segment 4 rarely tumescent behind; brood plates broadly subovate, 5th subequal, little reduced; coxal gills 3–5 little reduced; pleopod peduncles spinose, broadly sublinear; uropod 3 small; and telson lobes rarely with dorsal spines. Except for "Orchestoidea" *brasiliensis* (Dana), all other southern continental sandhoppers have a more or

less subchelate gnathopod 1 (♂), and antenna 2 and peraeopods 6–7 tend to be variously sexually dimorphic, and the bodies are smooth and eyes smaller. "Orchestoidea" *brasiliensis* is placed in a monotypic genus by Bousfield (1982 in prep.) because of its distinctive peraeopod 5 with reduced dactyl, and differing structure of gills, pleopods, and uropods.

Orchestoidea tuberculata Nicolet 1849
Figure 20

Orchestoidea tuberculata Nicolet 1849, p. 229, 231, t. 2, fig. 4
:Stebbing, 1906a, p. 527

Material examined

Chile: Cachagua, ocean beach at HW level, 13 November 1973, D.E. Dexter coll., 22 ♂♂ (to 21.0 mm), 45 ♀♀ (1 ov. several br. I and II) plus 5 imm., NMC-C-1981-519, slide mounts; Corral (near Valdivia), ocean beach, Lamb & Holz coll. (no data), 1 ♂ (19.0 mm), 2 ♀♀ ov. (16.0 mm); Playa Grande, Mehuin, Province Valdivia, June 1976, C. Varela coll., several imm. ♂♂ and ♀♀.
Peru: Mejia, near Mollendo (approx. 15°S, 72°W), 28 July 1957, H. Heller coll., several imm. ♂♂ and ♀♀, NMC-C-1981-518.

Remarks

The species bears a superficial resemblance to large, heavy-bodied sandhoppers of the North American Pacific coast. However, the numerous generically distinctive features (noted above and in the key) necessitate the removal of the boreal North American sandhopper complex from the genus *Orchestoidea* and resurrection of *Megalorchestia* Brandt 1851, to encompass them.

Distributional ecology

Occurs under drift debris at the HW level of surf-exposed, high salinity, cool temperate beaches of the Pacific coast of South America from south of Valparaiso to southern Peru (Mejia near Mollendo). No animals were taken on the beaches of the Cape Horn region during the Hudson 70 expedition (unpublished information); in that region, the dominant sand-beach amphipod is "Orchestia" *scutigerula* Dana.

Talitrus Latreille 1802

Talitrus Latreille 1802, vol. 1, p. 78, vol. 2, p. 148
:Stebbing, 1906, p. 524 (partim)
:Hurley, 1955, p. 145 (partim)
:Bulycheva, 1957, p. 127 (partim)
:Barnard, 1969a, p. 472 (partim)
Talitrus (*Talitrus*) Hurley 1975, p. 161

Diagnosis

Medium sized, heavy, smooth-bodied sandhoppers characterized by: head and buccal mass broadened below. Interior antennal sinus shallowly incised, deep to accommodate peduncle segment 1. Eyes medium, not dorsally contiguous. Antenna 1 short, peduncle 2 longest; flagellum shorter than peduncle. Antenna 2 elongate, peduncle longer in male but not incrassate. Mandibular left lacinia 5-dentate, proximal (5th) tooth small, right lacinia tricuspate. Maxilliped palp "tall", appearing 3-segmented, segment 2 broad, with spinose mediodistal lobe, segment 3 subconical, 4th (terminal) segment minute, masked by spines of segment 3. Coxa 1 deep, anterodistally acute. Coxae 2–4 subquadrate, cuspate behind. Gnathopod 1 simple, powerfully fossorial, larger in male; carpus elongate and heavily spinose; propod elongate, arcuate, narrowing distally, lacking palm; dactyl strong; propod and carpus lacking posterior tumescent process (♂, ♀). Gnathopod 2, propod mitten-shaped in both sexes; basis sublinear, somewhat more expanded antero-medially in female; segment 4 lacking posterior tumescent process; segment 5 tumescent postero-proximally; segment 6 shorter than 5. Peraeopods 3–7 cuspidactylate, segments stout, spinose, not elongate; dactyls medium. Peraeopod 4 shorter than 3, segment 5 distinctly shorter; dactyl short, prominently pinched, but not overhanging unguis. Coxa 5 aequilobate, lobes deep; coxa 6, hind lobe very deep, anterior margin vertical, rounding below. Peraeopods 5–7 weakly heteropodous in form, basis and segment 4 of short peraeopod 5 differing slightly from those of 6 and 7; peraeopod 6 longest. Abdominal side plates 1–3 deep, smooth below, weakly spinulose posteriorly; pleopods about normal, rami little reduced, multisegmented; peduncle sublinear, not expanded, outer margin short-spinose, inner with 2 retinacula. Uropods 1 and 2 stout, inner and outer

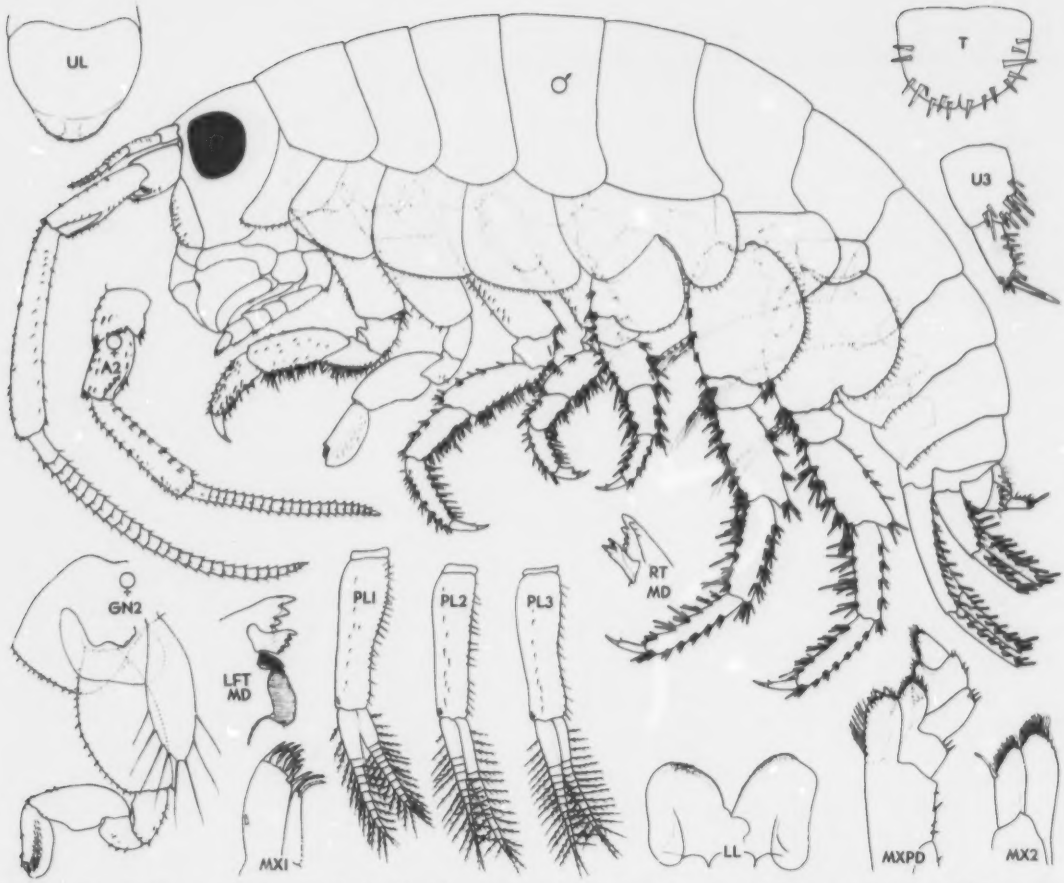

Figure 21. *Talitrus saltator* (Pallas). Northumberland, England. ♂ - 20.0 mm, ♀ ov. - 15.0 mm.

margins of peduncles and rami strongly spinose, terminal spines simple; uropod 2, outer ramus shorter than inner. Uropod 3 short, peduncle not broadened but spinose posterodistally; ramus cylindrical, tapering, short spinose behind, apical spine long. Telson short, broad; lobes nearly completely fused distally, with apical and marginal spines only. Coxal gills relatively large, somewhat sac-like, little reduced on peraeopods 3–5. Brood plates large, subovate, little reduced on peraeopod 5, marginal setae simple.

Type-species: *Talitrus saltator* Montagu 1808. (monotypic)

Remarks

The genus *Talitrus* is a true sandhopper, most closely allied with *Orchestoidea* Nicolet, and other 4-dentate genera; it is remote morphologically, as well as ecologically and behaviourally from the true landhoppers (Table IV, fig. 28). Despite the neotenic loss of amplexing type gnathopod 2 in the male (an advanced character that is convergently and superficially similar to that of many landhopper genera), *Talitrus* is plesiomorphic in several other taxonomic features, especially relative to those of large, stout-bodied sand hopper genera of North American coasts. (see Table III and fig. 27).

Talitrus saltator (Montagu 1808)
Figure 21

Talitrus saltator: Sars, 1895, p. 23, pl. 9
:Chevreux & Fage, 1925, p. 271, fig. 282

Material examined

England: Northumberland; sand beach, March 1955, D.I. Williamson coll., 5 ♂♂, 6 ♀♀ (3 ov.), NMNS Cat. No. 5014, slide mounts.

Portugal: Vila de Conde, A. Mateus coll. (no data), 2 ♂♂, 4 ♀♀, 2 imm., NMNS Cat. No. 10464.

Remarks

Although remote geographically from the North American Pacific coastal fauna, this northeastern Atlantic species is illustrated herewith to supplement the illustrations of Sars (1895), Bulycheva (1957) and others, in fully diagnosing the genus *Talitrus* and establishing more precisely its phyletic position among the Talitridae.

Pseudorchestoidea new genus

Orchestoidea: Bulycheva, 1957, p. 130 (partim)
:Bousfield, 1957, p. 120 (partim)
:Barnard, 1969a, p. 471 (partim)

Diagnosis

Small to medium, smooth, shallow-bodied, slender-legged sand hoppers characterized by: head and buccal mass shallow, inferior antennal sinus short, sharply incised. Eyes very large, bulging, nearly contiguous dorsally (especially male). Antenna 1 short, peduncular segments 2 and 3 subequal, flagellum shorter than peduncle. Antenna 2 slender, elongate (especially male), peduncular segments slender, not incrassate in male. Mandibular left lacinia 4-dentate, or with very weak 5th (proximal) tooth, right lacinia tricuspate; maxilliped palp tall, appearing 3-segmented, segment 2 with small mediodistal spinose lobe, segment 3 rounded-subconical, segment 4 minute (masked by spines of 3) or lacking. Coxa 1 shallower than 2–4, anterodistally subacute; coxae 2–4 shallow, wider than deep, hind margins cuspate. Gnathopod 1 (♂ and ♀) strongly fossorial, spinose; carpus elongate; propod distinctly shorter, lacking true palm; dactyl strong; carpus and propod with small posterior marginal blister in male only. Gnathopod 2 (♂) more or less powerfully subchelate (or neotenically arrested at partly transformed stage); propod ovate, palm usually oblique; dactyl strong, with posterior marginal process near hinge; gnathopod 2 (♀), basis short, expanded anteriorly; segment 3 short; 4 with small posterior tumescent process (occasionally also in male); 5 deeply tumescent behind; 6 mitten-like, subequal to 5, lobe well beyond dactyl. Peraeopods 3–7 slender, lightly spined, cuspidactylate, dactyls slender; peraeopod 4 slightly shorter than 3, segment 4 not greatly shortened, dactyl weakly pinched, body not overhanging base of unguis. Coxa 5 aequilobate, elongate, lobes shallow; coxa 6, hind lobe shallow, anterior margin usually oblique. Peraeopods 5–7 heteropodous, peraeopod 5 markedly shorter than, and basis and segments 3–6 of different form from, those of peraeopods 6 and 7; dactyl of 5 very short, thick, with "fuzz" setae posteriorly, nail vestigial; peraeopods 6 and 7 elongate, 7 longer. Abdominal side plates 1–3 medium deep, nearly smooth below and behind, hind corners acuminate. Pleopods slender; peduncles sublinear, elongate, inner margin with 2 retinacula, 2 and 3 always with outer marginal spines; rami subequal, multisegmented or partly reduced, shorter than respective peduncles. Uropods 1 and 2 slender, weakly spinose, with terminal spade spines; uropod 1, outer ramus bare, or with outer marginal spines only; prepeduncle of urosome 1 elongate; uropod 2, rami usually subequal, outer ramus with outer marginal spines only. Uropod 3 usually elongate, occasionally sexually dimorphic; peduncle not expanded but weakly spinose behind; ramus equal to or longer than peduncle, laterally compressed, margins and apex short-spinose. Telson usually narrowing distally, apex slightly notched or entire, lobes with short apical and dorsal spines. Coxal gills small, sinuous, those of peraeopods 3–5 smallest, that of peraeopod 6 not elongate. Brood plates small, narrowly ovate, smallest on peraeopod 5, margins distally and sparsely simple-setose.

Type-species: *Orchestoidea biolleyi* Stebbing 1908 (present selection)

Additional species:

Pseudorchestoidea brito (Stebbing 1891), p. 324, pl. 15

Pseudorchestoidea meridionalis (Schuster 1954)

Pseudorchestoidea gracilis (Bousfield & Klawe 1963)

Pseudorchestoidea mexicana new species (p. 50)

Etymology

The generic name is derived from the Greek "pseudes" meaning "false" and the root name *Orchestoidea*, and alludes to the mainly superficial similarity between the new genus *Pseudorchestoidea* and the true *Orchestoidea*. Gender: Feminine.

Remarks

The genus *Pseudorchestoidea* presently comprises three subgroups; the plesiomorphic *brito* group (monotypic) of the northwestern Atlantic and Mediterranean regions; the intermediate *meridionalis* group, containing three species, and the apomorphic monotypic *biolleyi* group, the latter two groups endemic to the Pacific coast of Central America and Mexico. The *brito* group is rather distinct from the other two groups (Table III and fig. 27) and links the genus to other sandhopper complexes, especially within the Indo-Pacific genus *Talorchestia*.

Key to species of *Pseudorchestoidea*

1. Antenna 2 relatively stout, some distal flagellar segments toothed behind; coxa 6, anterior margin of posterior lobe vertical, rounding; uropod 3 short, marginal and apical spines few, large; gnathopod 2 (♂), palm smoothly merging with posterior margin; eastern Atlantic ..... *P. brito* (Stebbing) (p. 48)
   Antenna 2 slender, distal flagellar segments not toothed (except *P. mexicana*); coxa 6, anterior margin of posterior lobe oblique, gently convex; uropod 3 elongate, marginal and apical spines small, numerous; gnathopod 2 (♂), propod with distinct prominence at posterior palmar angle; eastern Pacific 2
2. Peraeopods 6 and 7, bases relatively small, unlike in size and form; uropod 2, outer ramus distinctly shorter than inner; gnathopod 2 (mature ♂), propod small, short, weakly developed, posterior angle with prominent tumescent lobe (fig. 2,L). ..... *P. biolleyi* (Stebbing) (p. 53)
   Peraeopods 6 and 7, bases relatively large, subsimilar in size and form; uropod 2, rami subequal in length; gnathopod 2(♂), propod large, ovate, strongly developed, posterior angle with spinose prominence (fig. 2k) 3
3. Pleopod rami well developed, 12–15 segmented, little shorter than respective peduncles; uropod 1, outer ramus with marginal spines; antenna 1, flagellum 6–7 segmented, longer than peduncle 2 ..... *P. gracilis* (Bousfield & Klawe) (p. 49)
   Pleopod rami reduced, 4–10 segmented, much shorter than peduncles; uropod 1, outer ramus marginally bare; antenna 1, flagellum 4–5 segmented, about equal in length to peduncle 2 4
4. Dactyls of peraeopods 6 and 7, anterior margin pectinate (with several slender spines); peraeopods 6 and 7, bases rounded behind; uropod 1, inner ramus with medial (inner) marginal spines only; antenna 2 distal flagellar segments not toothed ..... *P. meridionalis* (Schuster) (p. 51)
   Dactyls of peraeopods 6 and 7, anterior margin with single distal slender spine; peraeopods 6 and 7, posterior margin of basis nearly straight; uropod 1, inner ramus with both inner and outer marginal spines; antenna 2 distal flagellar segments toothed..... *P. mexicana* new species (p. 51)

Pseudorchestoidea brito (Stebbing 1891)

Talorchestia brito Stebbing 1891, p. 324, pl. 15
:Chevreux & Fage, 1925, p. 279, fig. 279, 289
:Vader, 1970, p. 83, figs. 2–6
non *Orchestoidea brito*: Bulycheva, 1957

Material examined

England: Blyth, Northumberland county, sandy beach, March 1955, D.I. Williamson coll., 2 ♂♂, 1 ♀ ov., (to 11.5 mm), NMNS Cat. No. 5106, slide mounts.

Portugal: Sagres, sand beach, E. Mateus coll., (no other data), 5 ♂♂, (to 12.5 mm), NMNS Cat. No. 10465, slide mount.

Remarks

Vader (1970) has provided detailed figures of most of the important taxonomic characters omitted in the original description and by subsequent workers on material from the Atlantic-Mediterranean region. Compared to eastern Pacific species of the genus, *P. brito* is a heavier bodied animal, with stouter antennae, and stouter

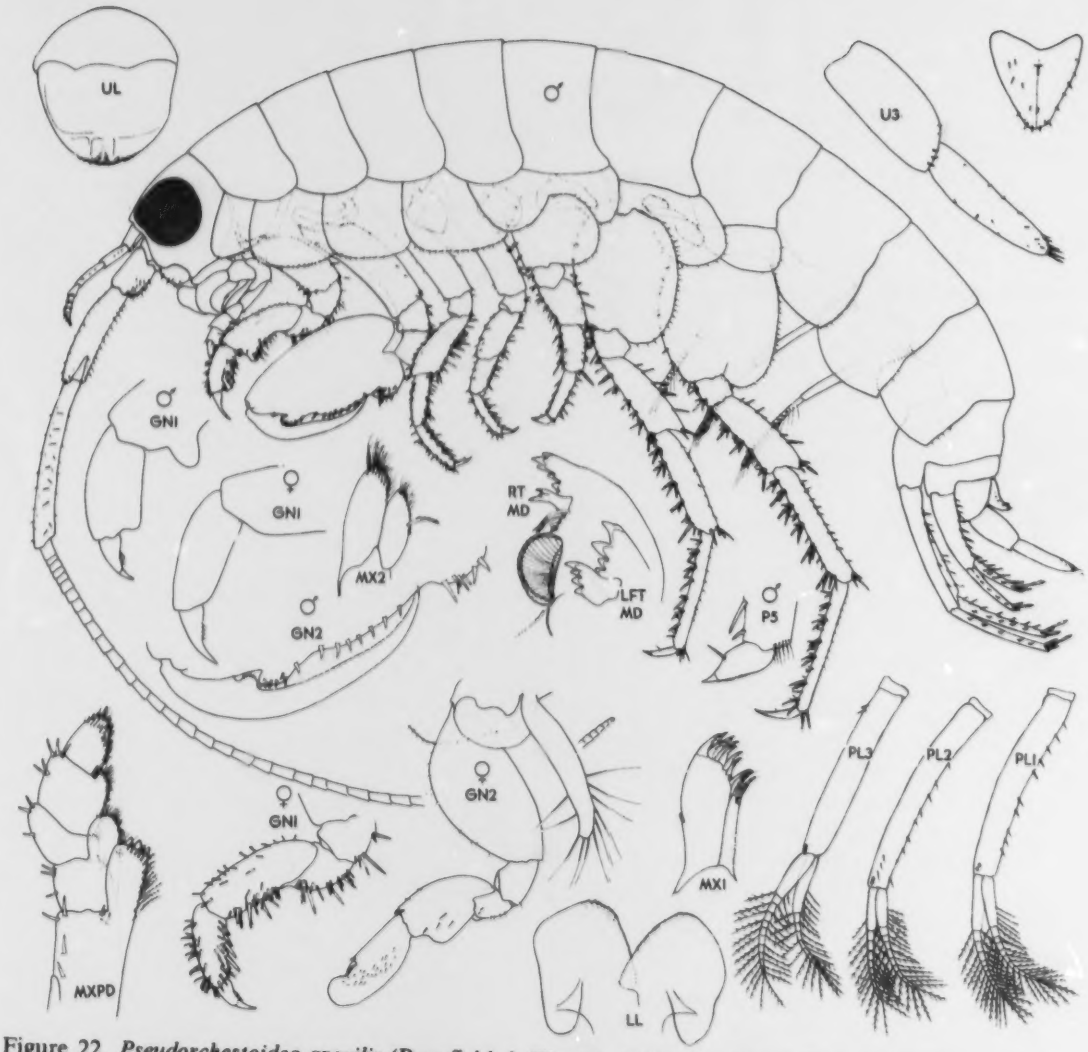

Figure 22. *Pseudorchestoidea gracilis* (Bousfield & Klawe). Cabo San Lucas, Baja California, Mexico. ♂ - 18.0 mm, ♀ ov. - 14.0 mm.

spines on uropods and peraeopods; the pleopods are less reduced; gnathopod 2, palmar margin merges smoothly with the posterior margin; and the ramus of uropod 3 is short, with a long terminal spine.

Distributional ecology

Occurs mainly on exposed, flat, sandy, high salinity, warm-water beaches, from southwestern Norway, along the European–Atlantic coast to Morocco and in the Mediterranean eastward to the Black Sea. The species is active on the beach by day, mostly lower on the shore than associated beach-hopper species, feeding mainly on unicellular algae, diatoms, and scavenging on animal carcasses, rather than on cast-up plant debris. Apparently cannibalism is common in *P. brito*. Females ovigerous in summer, May–September.

Pseudorchestoidea gracilis (Bousfield & Klawe 1963)
Figure 22

Orchestoidea gracilis Bousfield & Klawe 1963, p. 1, figs. 1, 2

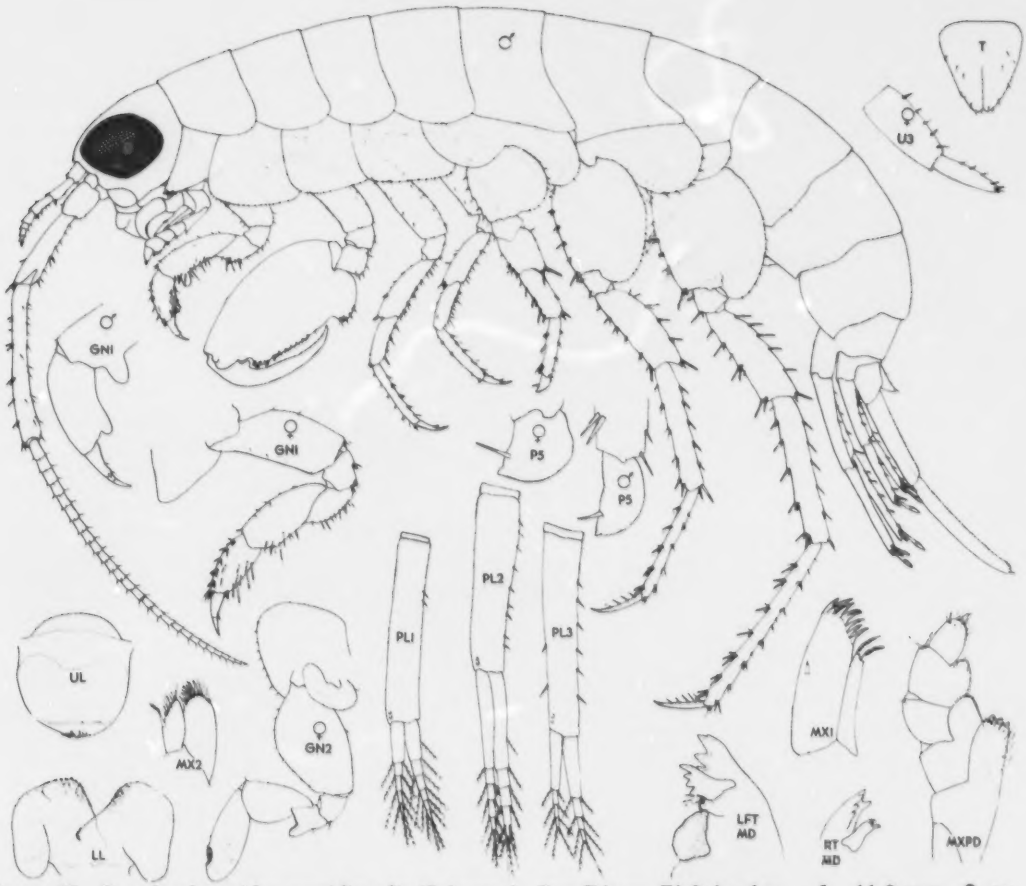

Figure 23. *Pseudorchestoidea meridionalis* (Schuster). San Diego, El Salvador. ♂ - 11.0 mm, ♀ ov. - 8.0 mm.

Material examined

Re-examination of Type and Allotype male and female and Paratype female material from a beach at Cabo San Lucas, Baja California, Mexico, NMNS Cat. Nos. 6634 and 6635, and slide mounts.

Diagnosis

Close to *P. meridionalis* Schuster and *P. mexicana* n. sp., in the following characters: eyes large, nearly dorsally contiguous; gnathopod 2 (♂) powerfully subchelate and amplexing in form; propod subovate, palm very oblique, with distinct tooth and depression hear hinge, and rounded spinose protuberance at posterior angle; posterior margin very short; peraeopods 6 and 7 very slender and elongate, 7 distinctly longer than 6 (especially in male), bases more or less rounded behind; uropods 1 and 2, spade spines strongly developed; uropod 3 elongate and sexually dimorphic; and telson tongue-shaped, narrowing distally. Differing from *P. meridionalis* and *P. mexicana* in the more elongate antenna 1 (flagellum 6–7 segmented), smaller, more quadrate eye; more strongly spinose peraeopods, shorter (non-pectinate) dactyls of peraeopods 6 and 7; larger basis and dactyl of peraeopod 5; more elongate pleopods; more heavily spinose uropods 1 and 2, in which the outer ramus of uropod 1 is marginally spinose; and the shorter, less sexually dimorphic uropod 3. The group of *P. gracilis*, *P. meridionalis* and *P. mexicana* is slightly more plesiomorphic than *P. biolleyi* Stebbing, but more apomorphic than the larger

European *P. brito* in which the eye is smaller, peduncle of antenna 2 (♂) somewhat thickened, gnathopod 2 (♂) palm less strongly toothed and less oblique; peraeopods 6 and 7 not very elongate or differing markedly in length; uropod rami shorter but more strongly spinose; uropod 3 very short; and telson subquadrate.

Distributional ecology

Occurs on open and semi-protected beaches of southern Baja California, burrowing in the upper tidal sand by day, and actively foraging at night over the entire beach, especially on the wet sand near the water's edge. Animals are occasionally bioluminescent, presumably derived from luminescent bacteria in the food.

Pseudorchestoidea meridionalis (Schuster 1954)
Figure 23

Orchestoidea meridionalis Schuster 1954, p. 103, fig. 1
:Bousfield & Klawe, 1963, p. 2 (key)

Material examined

San Diego, Department La Libertad, **El Salvador**, sandy beach, upper tidal zone, 24 November 1957, O. Schuster coll., 1 ♂ (11.0 mm), 5 subadult ♂♂, 3 ♀♀ subadult, 1 imm. ♀. NMNS Cat. No. 5851, slide mount.

Diagnosis

As diagnosed in the key, in morphological comparison with *P. gracilis* and *P. mexicana* (above) and as illustrated. Also, sexual dimorphism was noted in the form of the abbreviated dactyl of peraeopod 5, which is more elongate and less swollen in the male. Gnathopod 2 (♀), basis is strongly expanded anteriorly, and the propod is distinctly longer than the carpus, the minute dactyl located about ⅓ from the apex. Antenna 2 flagellum distal segments simple, not shortened or toothed.

Distributional ecology

Known only from surf-exposed sandy beaches of El Salvador, Pacific coast of Central America (Schuster, 1954), in the upper third of the tidal zone.

Pseudorchestoidea mexicana new species
Figure 24

Material examined

Mexico: Mazatlan, Sinaloa Province, on sand beach near HW level, G.A. Cole, coll., 6 August 1969. Female Holotype, br. II, 10.0 mm, subadult male Allotype, 8.5 mm; female, br. II, Paratype; adult male (anterior peraeonal region only) Paratype. NMC-C-1981-507. *Ibid*, lot No. 2. In crab burrows at HW level, 2 ♀♀ (br. I and II); Paratypes NMC-C-1981-507. Santiago Bay, Department Colima, sand beach, 29 January 1964, W.L. Klawe coll., 1 ♂ subad. (9.0 mm), 1 ♀ br. II (11.0 mm), 1 imm., NMC-C-1981-508.

Diagnosis

Female (br. II, 10.0 mm). Slender-bodied, slender-legged, sandhopper characterized by: eyes very large, rounding above and nearly contiguous mid-dorsally; antenna 1 very short, flagellum 4–5 segmented, about equal to segment 2 of peduncle; antenna 2 slender, distal 7–8 segments somewhat shortened, sharply toothed behind. Mandible, left lacinia cleanly 4-dentate; maxilliped palp, segment 3 slightly longer than wide. Coxa 1, anterodistal angle subacute. Gnathopod 1, propod elongate, posterior margin about ⅔ length of anterior margin. Gnathopod 2, basis broadly expanded anteromedially, segment 4 with prominent posterior tumescent lobe. Peraeopods 3–7 very slender, relatively weakly spinose; dactyls slender, those of peraeopods 6 and 7 with single anterodistal slender spine; peraeopod 5, dactyl very abbreviated and stout, basis asymmetrically broadly rounding behind; peraeopods 6 and 7, basis relatively large and subsimilar, posterior margins nearly straight, weakly spinose. Abdominal side plates smooth below and nearly unarmed behind; pleopods very slender, 1 shortest; rami much reduced, 4–6 segmented; peduncle of 1, outer margin spinose proximally, of 2 and 3 short-spinose distally. Uropods 1 and 2 slender, weakly armed, terminal spade spines well developed; uropod 1, outer ramus lacking marginal spines, inner ramus with inner (medial) marginal spines and a few proximal medial marginal spines; uropod 2, rami subequal, inner ramus with both margins spinose, outer ramus with outer marginal spines only. Uropod 3 elongate, peduncle weakly short-spinose distally, ramus longer, laterally compressed, with short facial and apical spines. Telson short, tapering broadly, apex notched, lobes with a few dorsolateral and apical short spines. Coxal gills

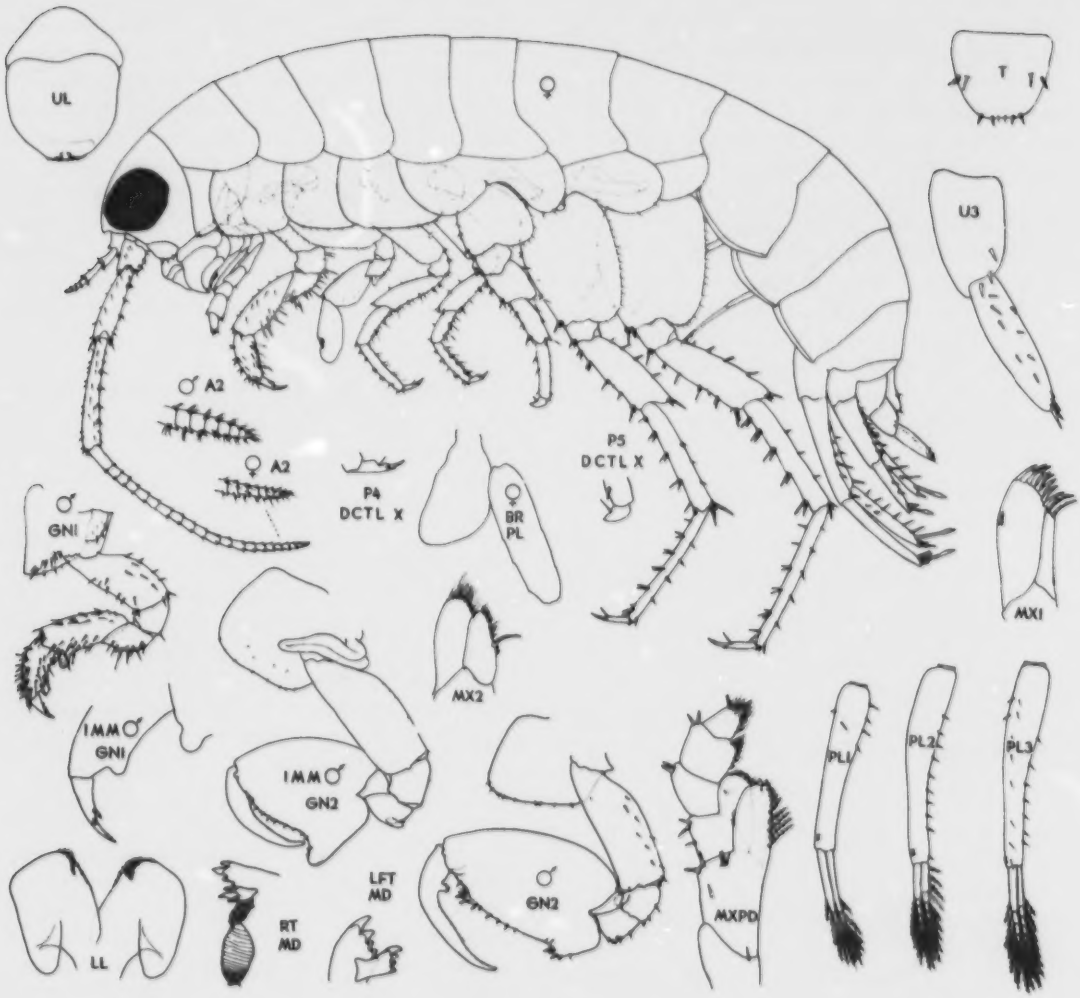

Figure 24. *Pseudorchestoidea mexicana* new species. Mazatlan, Mexico. ♀ br. II. - 10.0 mm, ♂ subad. - 8.5 mm, ♂ adult (gnathopods only)-

small, normal, 6 not elongate. Brood plates not fully developed, lacking setae in material available.

Male (8.5 mm) Allotype. Very like the female except gnathopod 1, carpus and propod tumescent behind, blister of propod subterminal. Gnathopod 2 in transforming stage, posterior margin of basis with 6–8 scattered spines, segment 4 with posterior process; propod small, palm smoothly convex, with small depression near hinge; dactyl short, tip reaching base of posterodistal palmar tumescence.

Presumed mature male Paratype (length unknown). Gnathopod 2, basis with anterodistal lobe; propod large, powerful, palmar margin very oblique, spinose, with large hinge tooth and depression and spinose posterodistal prominence; dactyl hind margin weakly spinulose, with prominent hinge tooth.

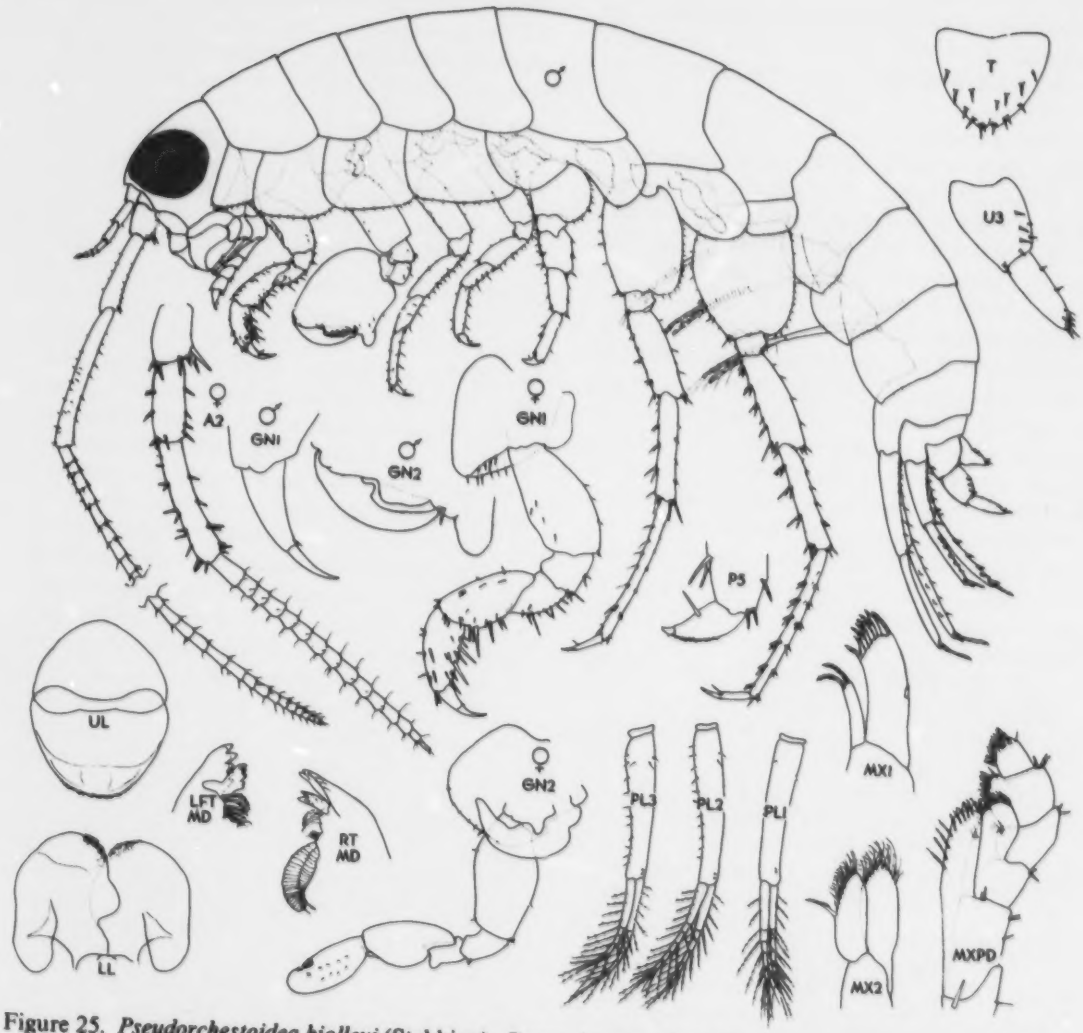

Figure 25. *Pseudorchestoidea biolleyi* (Stebbing). Punta Arenas, Costa Rica. ♂ - 12.5 mm, ♀ - 8.5 mm.

Remarks

Closely allied morphologically to *Pseudorchestoidea meridionalis* and *P. gracilis*, as described above, in the key (pp. 71–73) and as illustrated; more closely similar to *P. meridionalis* in size; eye shape; short flagellum of antenna 1; very reduced dactyl of peraeopod 5; reduced rami of pleopods (4–6 segmented vs. multi-segmented); unarmed outer ramus of uropod 1; shorter telson, and less heavily spinose appendages. *P. mexicana* differs from *P. meridionalis* mainly in the smooth (vs. pectinate) dactyls of peraeopods 6 and 7; the more nearly straight posterior margins of the basis of peraeopods 6 and 7; the more strongly spinose pleopod peduncles; and more heavily spinose rami of uropods 1 and 2 (inner ramus of uropod 1 with both inner and outer marginal spines). Sexual dimorphism in uropod 3 could not be determined from the material available.

Etymology

The specific name refers to the Pacific mainland coast of Mexico, the type locality of the species.

Pseudorchestoidea biolleyi (Stebbing 1908)
Figure 25

Orchestoidea biolleyi Stebbing 1908, p. 241, figs. 1, 2
:Bousfield & Klawe, 1963, p. 2 (key)

Material examined

Costa Rica: Airport Beach, Limon (98°58'N, 83°01'W) 19 March 1971, D.M. Dexter coll., 1 ♂, 5 ♀♀, 2 ov. (to 11.0 mm), 3 imm. 1 juv., NMC-C-1981-514; Playita Blanca, Playas del Coco, (10°34'N, 85°42'W), 9 February 1971, D.M. Dexter coll., 3 ♂♂, 8 ♀♀, 9 imm. NMC-C-1981-512, Naos Is., sand beach, 19 June 1973, D.M. Dexter coll., 2 ♂♂ (to 12.0 mm), 4 ♀♀, 13 juv., NMC-C-1981-516; Puerto Columbia, sand beach, 12 April 1971, D.M. Dexter coll., 1 ♂ transf. NMC-C-1981-513; Punta Arenas, sandy beach, under logs and driftwood, 26 November 1959, W.L. Klawe coll.; Lot No. 1, 2 ♂♂ (to 11.5 mm), 1 ♂ transf., 1 ♀; Lot No. 2, 1 ♂, 1 ♂ transf., 3 ♀♀ subad., 3 imm., 2 juv., NMNS No. 5862.

Diagnosis

Small, slender bodied, long-legged, weakly spinose sandhoppers, closely allied to the *meridionalis* group in having large, nearly dorsally contiguous eyes; slender antenna 2, flagellar segments simple (not toothed behind); elongate peraeopods (7 distinctly longer than 6); uropods 1 and 2, slender, elongate; prepeduncle elongate; ramus of uropod 3 elongate, short-spinose and laterally compressed; and telson distally narrowing. *P. biolleyi* is distinctive in the following characters; maxilliped palp, segment 3 as long as wide, rounding apically; mandibular left lacinia with small proximal (5th) tooth; gnathopod 1 (♀), propod relatively short, posterior margin of carpus about half anterior; gnathopod 2 (mature ♂) weakly subchelate, propod small, neotenically arrested at transforming stage; gnathopod 2(♀), basis moderately expanded anteriorly; segment 4, posterior process short; peraeopod 5 very small, short, basis rounding behind; peraeopods 6 and 7, bases relatively small, more or less unlike in size and form, hind margin of 7 nearly straight; dactyls slender, not pectinate anteriorly; pleopods slender, rami multi-segmented, little reduced; peduncle of 1 not markedly shorter than 2 and 3, outer margins of 1 smooth. Uropods 1 and 2 weakly spinose, terminal spade spines sublinear; uropod 1, outer ramus lacking marginal spines; uropod 2, outer ramus distinctly shorter than inner (especially in male), inner ramus with inner marginal spines only. Uropod 3 not markedly sexually dimorphic. Telson short spade-shaped, with scattered small dorsal spines.

Distributional ecology

Known only from sandy beaches of the Pacific coast of Costa Rica and Panama, in the upper tidal zone. Females ovigerous in late winter and spring; probably two or more broods per year.

Pseudorchestoidea spp.

Single immature specimens probably referable to this genus, but not identifiable to species, have been examined from the following localities:
1. Isla Grande, Mexico: Stn. 5 (no further data), 1 subad. ♂ (10.0 mm). NMC-C-1981-460, slide mount. The specimen corresponds with the type material of *P. mexicana* in the weakly spinose uropods (uropod 1 outer ramus marginally bare), weakly armed distal segments of peraeopod 5, non-pectinate peraeopod dactyls, reduced rami and proximally spinose margins of peduncle 1 of the pleopods, but differs in the larger number of segments in the pleopod rami (6–10, vs. 4–7), the lack of teeth on the distal segments of the flagellum of antenna 2, and the more distal position of the posterior tumescent lobe of the propod of gnathopod 1.
2. Ensenada, Baja California, Mexico: Under seaweed at HW line, sand beach, 3 June 1956, W.L. Klawe coll., 1 imm. ♀ (5.5 mm), NMC-C-1981-464, slide mount. This very immature specimen is clearly a sandhopper close to *Pseudorchestoidea* in overall facies, including slender peraeopods 6 and 7 of which 7 is the longer; slender pleopods; short palmless propod of gnathopod 1; slender, weakly armed uropods 1 and 2; 4-dentate mandibular left lacinia; and spade-shaped, distally notched telson, among other features. However, the relatively unmodified peraeopod 5, the dactyl of which is of normal length, but with "fuzz" setae on the posterodistal margin, the nearly unarmed margins of the pleopod peduncles, and the short ramus of uropod 3, are more like Caribbean species of *Talorchestia*.

The presence of these single enigmatic specimens, and the distributionally limited material of this study, underscore the need for more intensive collecting of amphipods along the beaches of Mexico and Central America in order to delimit more fully the diversity and phyletic relationships of the regional Talitridae.

Section III. Landhoppers

Truly terrestrial amphipods are not native to the North American Pacific coastal or inland continental regions. Native terrestrial species are known, however, from Central America, including Costa Rica and Panama (Bousfield, in prep.)[1], from the Galapagos (Bowman, 1977), from Hawaii and the north central Pacific Islands (Bousfield & Howarth, 1976) and from western Pacific coastal regions, especially Japan (Iwasa, 1939; Tamura and Koseki, 1974). Absence of native cool-temperate landhopper species in coastal rainforests of the North American Pacific coastal regions contrasts with the rich landhopper faunas of climatically similar forested land regions of the southern hemisphere such as South Island, New Zealand, and Tasmania (see Hurley, 1955, 1968; Friend, 1980). These populations have been explained on the basis of a probable Gondwanaland origin of primary terrestrial groups, and coincidental evolution of angiosperm leaf litter, subsequent continental drift, and evolution of other regional landhopper groups from immediate seashore progenitors (Bousfield, in press)[1]. Thus, native landhoppers of the Central American, Hawaiian, and Japanese coastal continental rain forests are of the cuspidactylate (modern) type and related morphologically to local seashore (beach flea) types. Synanthropic populations of a few landhopper talitrids have been recorded in parks, botanical gardens, and zoological gardens of coastal cities of California (records summarized in Bousfield, 1975; Biernbaum, 1980).

Non-cuspidactylate (ancient) types, such as *Arcitalitrus dorrieni* (Hunt), and *A. sylvaticus* (Haswell) have relatively low eurytopicity and when introduced by man to new habitats of the northern hemisphere, the amphipods spread slowly or remain in place (Richardson, 1980). On the other hand, cuspidactylate types such as *Talitroides alluaudi* Chevreux, and *T. topitotum* (Burt) seem much more hardy and may spread rapidly from their points of introduction, especially in coastal, winter-mild continental areas and on tropical islands (Bousfield & Howarth, 1976; Biernbaum, 1980).

Key to introduced terrestrial amphipods of North America

1. Peraeopods 3–7 cuspidactylate; peraeopod 4 shorter than 3, segment 5 shorter than and dactyl different from those of peraeopod 3 respectively; coxal gill of peraeopod 6 reverse L-shaped or curved forward ..... *Talitroides* 2
   Peraeopods 3–7 non-cuspidactylate (simplidactylate); peraeopods 3 and 4 subequal, segments 5 and dactyl similar in size and form; coxal gill of peraeopod 6 goose-necked, attenuated posteriorly ..... *Arcitalitrus sylvaticus* (Haswell) (p. 55)
2. Antenna 1 elongate, nearly reaching tip of peduncle 5 of antenna 2; uropod 1, distolateral (interramal) spine with complex tip ..... *T. topitotum* (Burt) (p. 55)
   Antenna 1 shorter, tip reaching about mid-point of peduncle 5 of antenna 2; uropod 1, distolateral spine with simple tip ..... *T. alluaudi* Chevreux

Arcitalitrus sylvaticus (Haswell 1880)

Talitrus sylvaticus Haswell 1880, p. 246, pl. VIII, fig. 1
:Bousfield & Carlton, 1967, p. 282
:Bousfield, 1975, p. 353 (key), 364

Distributional ecology

Recorded in North America only from leaf litter (mainly *Eucalyptus*) and damp debris in Golden Gate Park, and adjacent areas of San Francisco, California; endemic to southeastern Australia (New South Wales and Victoria). No additional regional material has been examined since the records of Bousfield & Carlton (1967).

Talitroides topitotum (Burt 1934)

Talitropsis topitotum Burt 1934, p. 184, fig. 11
:Vader, 1972
Talitrus decoratus Carl 1934, p. 134, p. 742, figs. 1–6
Talitrus pacificus Hurley 1955, p. 155, fig. 3
Talitrus sylvaticus Shoemaker, 1936, p. 60, fig. 1

[1]Bousfield, E.L. A revised classification of Talitrid amphipods (Crustacea: Amphipoda: Talitridae). (In prep.)

"*Talitrus*" *sylvaticus*: Bousfield, 1975, p. 353 (key), 364, fig. 231

Material examined

California: Balboa Park, San Diego Co., mixed litter, *Eucalyptus* and *Pittisporum*, near zoo, 23 February 1978, K.K. Bohnsack coll., 20 ♀♀. br. I and II (to 9.5 mm). NMC-C-1981-547.

Distributional ecology

In leaf litter and under moist garden debris, along the Gulf coast of the United States from Louisiana east to Florida and north to South Carolina; in California, authentically recorded only from Balboa Park, and Pasadena, but probably occurring in the San Francisco Bay area also. Bierbaum (1980) has summarized records in North America and world-wide.

Discussion and Conclusions

The present generic revisionary concepts within the family Talitridae are based mainly on analysis of character states within North Pacific and selected world-wide species and higher groupings, as summarized in Tables I, II, III, and IV. The cluster analysis and resulting phenograms (figs. 26, 27, 28) complement the results of a revision[1] of world-wide Talitridae recently completed by the writer (Bousfield, in prep.).[2] The phyletic (evolutionary) conditions of morphological characters used in this analysis are differentiated within each table by the symbol 0 (plesiomorphic) or 1 (apomorphic). These conditions (subject to confirmation in some instances) were derived by comparison with related outgroups in presumed ancestral families Hyalidae, Hyalellidae, Najnidae and palustral Talitridae (see Bousfield 1981, in prep.).[3] [2] Thus, an index of plesio-apomorphy is obtained by totalling the numbers for all character states for each species; low total values characterize primitive or plesiomorphic, and high numbers the advanced (derived) or apomorphic taxonomic groupings. An attempt was made to select or define characters that would minimize instances of the intermediate condition across the taxonomic spectrum; such cases were slotted into either the primitive or advanced category (a taxonomic judgment) in order to utilize a simplified two-stage average linkage cluster analysis (Sneath & Sokal 1973).

The total body analysis more clearly reveals evolutionary trends in talitrid subgroups, morphological relationships that were generally masked by previous reliance on a few characters (especially of the gnathopods, some mouthparts, etc.) for generic (Bulycheva 1957), or subgeneric (Hurley 1975) delineation. Thus the transcending significance of condition of peraeopod dactyls and dentition of the mandibular left lacinia mobilis, the more precise definition of character states within the mouthparts, gnathopods, uropod 3 and telson, and recognition of significant new character states within the antennae, coxal plates, peraeopods, pleopods, uropods 1 and 2, gills and brood plates have collectively necessitated reassessment of generic groupings within the family. Most previously accepted full genera have been validated herewith, but in a more restricted sense, and based on the type species in each case. Some generic names, previously synonymized, have been resurrected, a few subgeneric names have been elevated to full generic status, several new generic names have been created, and all species have been reassigned within the old and new generic concepts. Taxonomic characters proposed herewith are at a level of taxonomic significance similar to those utilized in recent revisions of amphipod family and superfamily groups of the North Pacific region (e.g., Bousfield, 1979b (Gammaroidea); Conlan & Bousfield, 1982, (Ampithoidae)); and of other regions (Friend, 1980 (terrestrial Talitridae)).

Formal recognition of the broad systematics-ecological units of Talitridae employed here is compromised by morphological convergences on the one hand, and ecological overlap on the other. Now required is a refinement of the system that will satisfactorily deal with these limitations and avoid formalization of polyphyletic groupings, as in the past. Also required is much more information on the functional morphology and behaviour of these animals. Even with these limitations, the present system provides a basis for more natural grouping of species and genera, and new insights into the probable evolutionary history of the Talitridae. Thus, within the beach flea group (Table II, and fig. 26), the North Pacific rim region encompasses native genera (*Traskorchestia*, *Paciforchestia*) that are primitive relative to those of the North Atlantic and tropical-warm-temperate regions (*Orchestia* sens. str., "Orchestia" *floresiana* group) but are comparably apomorphic to those of antiboreal (southern hemisphere) regions (e.g., *Protorchestia*, *Transorchestia*). The North Pacific also encom-

[1]Elements of this revision were presented orally at a Symposium on Biogeography, Annual Meeting of the Canadian Society of Zoologists, University of Waterloo, May 1981.

[2]Bousfield, E.L. A revised classification of Talitrid amphipods (Crustacea: Amphipoda: Talitridae). (In prep.)

[3]Bousfield, E.L. The amphipod superfamily Talitroidea in the northeastern Pacific region: 2. Family Hyalidae. Systematics and distributional ecology. (In prep.)
Bousfield, E.L. The amphipod superfamily Talitroidea in the northeastern Pacific region: 3. Family Najnidae. Systematics and distributional ecology. (In prep.)

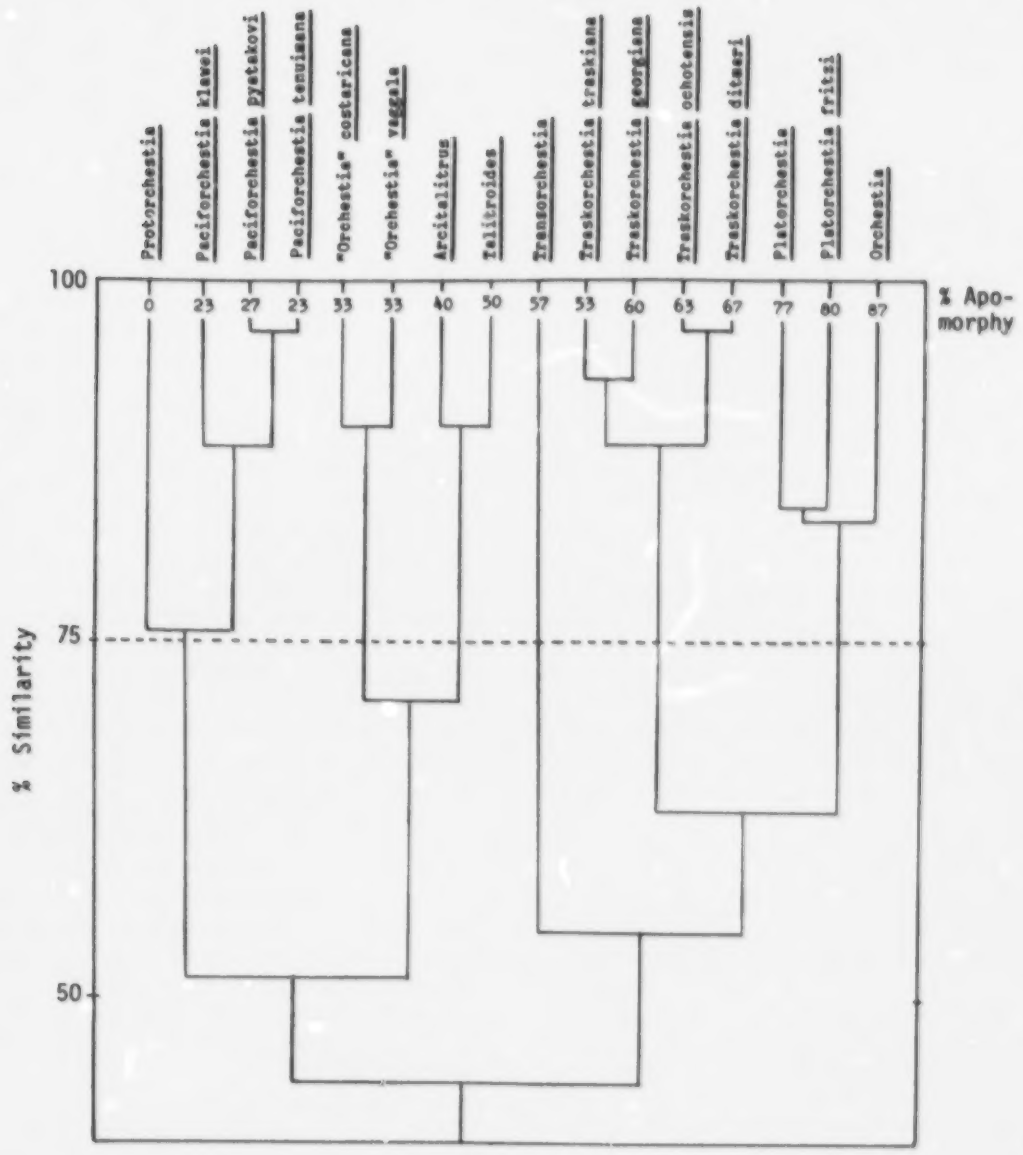

Figure 26. Phenogram of Species of Beach Fleas, Palustral Talitrids, and Landhoppers, North Pacific Rim region, and other related groups.

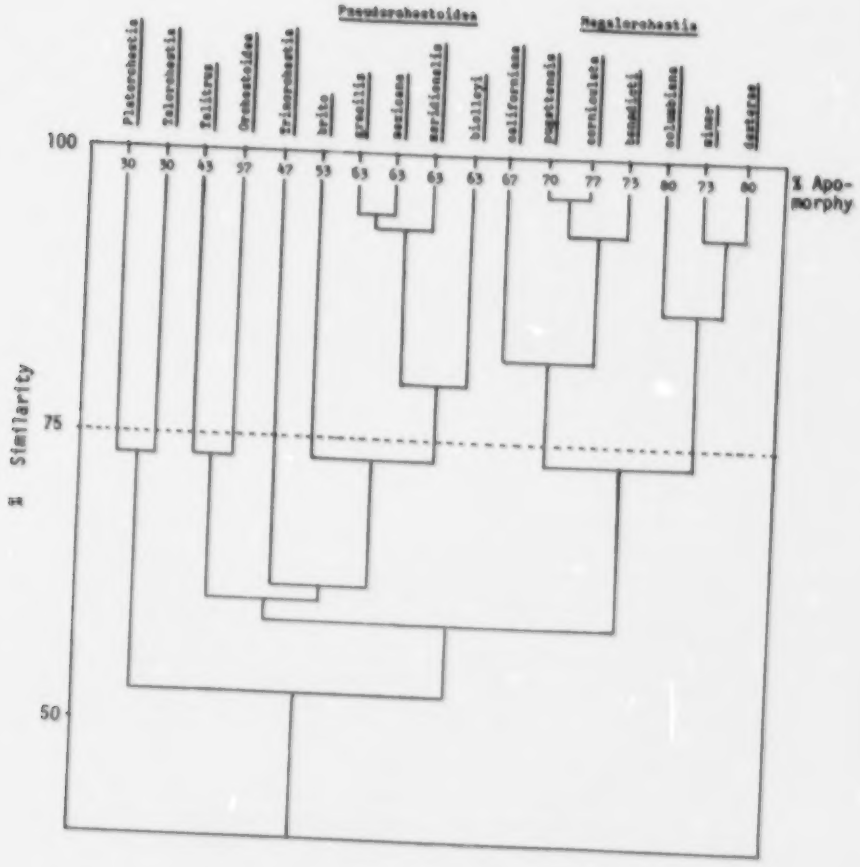

Figure 27. Phenogram of Species of Sandhoppers, North Pacific Rim Region, and other related groups.

passes the genus *Platorchestia*, most species of which trend to a fossorial mode of life on sandy beaches; thus *Platorchestia* may be close to the presumed ancestor of most 5-dentate, heavy-bodied, cold-temperate sandhoppers of the northern hemisphere (see also Table III and figs. 27, 28). Paradoxically perhaps, North Pacific rim sandhoppers, especially those of the North American coast, are generally apomorphic, and component members (*Megalorchestia*, *Pseudorchestoidea*) are among the world's most specialized sandhoppers. The phenograms (figs. 27, 28) confirm the need for formal recognition of the new generic categories and more natural realignment of key genera (e.g., *Talitrus* with *Orchestoidea*; *Megalorchestia* with *Trinorchestia*, *Talorchestia*, and *Platorchestia*; *Pseudorchestoidea* with Caribbean members of *Talorchestia*), as outlined also by the author elsewhere (Bousfield, in prep.)[1]. Formal recognition of subgroups within sandhopper genera (e.g., within *Megalorchestia*)[2]

[1]Bousfield, E.L. A revised classification of Talitrid amphipods (Crustacea: Amphipoda: Talitridae). (In prep.)

[2]Similarly, the 8 species of "Talorchestia" sandhoppers recorded from New Zealand by Hurley (1956) comprise three or four distinctive morphological and ecological-behavioural groups that require further analysis and probable generic recognition.

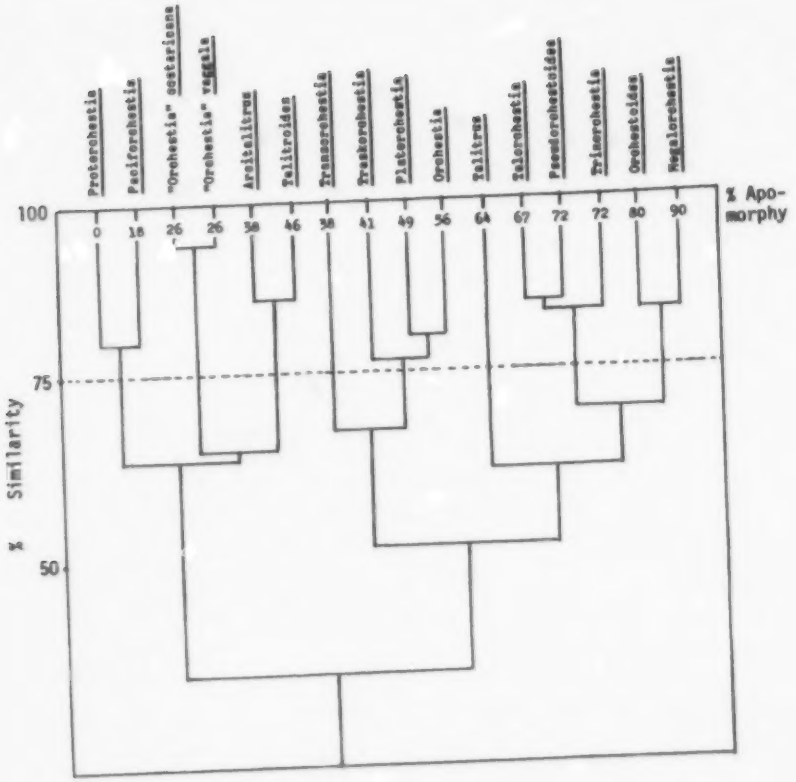

Figure 28. Phenogram of Genera of all Groups of Talitridae, North Pacific Rim Region, and other related genera.

awaits more intensive study of functional morphology, behaviour, and the life histories of component species (e.g., Morino 1978, Bowers, 1964).

The distributions of 37 species of Talitridae in the North Pacific region have been summarized in Tables V and VI. The gross Pacific rim coastline has been subdivided into 15 sub-regions that more or less reflect existing coastal marine biogeographic provinces (see Brusca & Wallerstein, 1979, Tzvetkova, 1975). Distributional data for beach fleas and landhoppers reveal that highest numbers of species occur on the North American coast in zones 11 and 12, on either side of 35°N latitude, and on the Asiatic coast in zones 1 and 2, at comparable latitudes, and in comparable numbers; numbers of species decrease both north and south of those zones. For the sandhoppers, a similar pattern emerges, for similar numbers of species. Total numbers (including introduced species in North America) also confirm this trend. Thus, fewest species of Talitridae (4/37) have been recorded from the vast 5000 km coastline from Kamchatka to Northern British Columbia. Low species numbers in the Cortez and Mexican provinces undoubtedly

reflect inadequate sampling and suggest that further collecting along the Baja and mainland Mexican coasts would yield much new distributional, and probably also taxonomical, information.

As noted previously (Bousfield, 1979c; 1981), the northernmost species (e.g., *T. traskiana*, *M. pugettensis*, and *M. columbiana*) tend to be the most plesiomorphic within their generic and subgeneric groupings, and also tend to be the widest ranging and most eurytopic species. Conversely, the most apomorphic species within these same groupings tend to be the most southerly in distribution and have the narrowest latitudinal ranges (e.g., *T. ditmari* and *T. georgiana* within the genus *Traskorchestia*, and *M. benedicti* in the *Megalorchestia pugettensis* group).

Of primary significance in the evolution of terrestrial amphipods may be the total lack of native terrestrial Talitridae in the North American coastal region, despite their presence in Central America, Cocos Is., Galapagos Is., Hawaii, and Japan (Table VI). This hiatus is not plausibly explained solely in terms of centres of origin and continental drift dispersal (see also Bousfield 1982, in press). Land amphipods in all peripheral Pacific regions above are "modern" cuspidactylate types, closely related to regional seashore species groups (e.g., *P. japonica* to *P. platensis* in Japan, "Orchestia" *pickeringi* to "Orchestia" *floresiana* in Hawaii, etc.); thus, terrestrial evolutionary potential is presumably present in North America also.

Land amphipods may have evolved in concert with the evolution of angiosperm leaf litter, the preferred food in continental deciduous rain forests of Tasmania and Victoria (Friend, 1980). However, the rain forests of the North American Pacific coast at comparable latitudes and with comparable winter-mild climates are today essentially climax-coniferous, and their forest floor organic debris is singularly deficient in deciduous (angiosperm) leaf litter. In this important respect they contrast markedly with rain forests of other peripheral North Pacific regions, and with those of Tasmania and Victoria, where conifers are relatively rare or lacking, and deciduous leaf litter is predominant and renewed seasonally as food for the amphipods. Paratropical rain forests, including feather palms, fan palms, and mangroves apparently existed along the Pacific Northwest coast (northeastern California to northwestern Washington and S.E. Alaska) during warm moist Eocene climates and became predominantly broad-leaved deciduous during the cooler Oligocene (Wolfe, 1978). Penetration of Palaeocene leaf litter habitats by terrestrial amphipods may never be known with certainty; the cooling climates and decreasing deciduous forests of the Neogene to Recent eras would have been unfavourable for them, and none occur there today. Indirect evidence of possible former occurrence might be obtained through analysis of feeding types among the regionally endemic isopods, myriapods, and other leaf litter arthropods that normally occur in association with terrestrial amphipods.

Finally, palustral amphipods having immediate common ancestry with non-cuspidactylate "ancient"-type landhoppers (Table II and fig. 26) are known only from the Central American and northern South American coasts of the eastern Pacific, presumably northward to the limit of mangrove swamps in Mexican and Cortez provinces, and unknown north of those regions where native *Spartina* salt marshes are also rare or totally lacking. Pertinently, "Orchestia" *vaggala* Bowman 1977, the only known terrestrial amphipod from the evolutionarily isolated Galapagos Islands in the eastern Pacific, is very closely related to the chelate (apomorphic) palustral talitrids (e.g., *O. costaricana* Stebbing) endemic to salt marshes and mangrove swamps of the Caribbean region (Table II, fig. 26), but not terrestrial there. Perhaps the North American Pacific palustral or beach flea counterpart with terrestrial potential is the very plesiomorphic *Paciforchestia klawei* (fig. 26) whose western Pacific analogues (*P. tenuimana* and possibly "*P.*" *kokuboi*) have invaded truly terrestrial habitats in the southern islands of Japan.

Acknowledgments

The accumulation of extensive material required for this study has required the generous cooperation of many organizations and individuals. Appreciation to the many agencies and colleagues who collaborated in the field has been accorded in several pertinent publications (see especially Bousfield & Jarrett 1981) and is herewith again gratefully acknowledged. Several colleagues have contributed valuable suggestions and insights into talitrid taxonomy and biogeography over the years, some of which is embodied inextricably herewith; I refer especially to past exchanges with Drs. T.E. Bowman, J.L. Barnard, and the late C.R. Shoemaker, Smithsonian Institution, Washington; Dr. Wim Vader, Tromsø, Norway; Dr. A.M.M. Richardson and Dr. A.J. Friend, Hobart, Tasmania; Dr. Hiroshi Morino, Mito, Japan; Dr. N.L. Tzvetkova and the late Dr. E.F. Gurjanova, Leningrad, USSR; Dr. J. Carlton, Woods Hole, Mass.; Dr. D.M. Dexter, San Diego State College, California; Dr. D.E. Hurley, Wellington, New Zealand; and museum colleagues Dr. J.J. Dickinson and Mrs. D.R. Laubitz. Loan or donation of additional study lots has been noted in the accounts of material examined, but for much adventitiously collected material a note of special appreciation is made to Dr. W. Klawe, La Jolla, California, Mr. Craig P. Staude, Friday Harbor Laboratories, Drs. Stewart and Jarmila Peck, Carleton University, Ottawa, Dr. Daryl Bowers, Oakland, Calif.; Mrs. J.F.L. Carl, Victoria, B.C., and Dr. D.M. Dexter. Most of the line drawings were rendered by Mrs. F.E. Zittin, Vancouver, B.C., supplemented with a few illustrations by Mr. C. Paquette, Ottawa, Mr. C. Douglas, NMNS staff artist, and the author.

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Table 1. Major Taxonomic Characters of Family Talitridae and Their Plesiomorphic and Apomorphic States*

No.	Taxonomic Character	Phyletic State: Plesiomorphic	Phyletic State: Apomorphic
1.	Eye size and position	Medium, lateral	Large, dorsally contiguous; *very small or lacking.*
2.	Antenna 1, length	Elongate, equal to or exceeding A_2 peduncle 4	Short, not reaching end of A_2 of peduncle 4
3.	Antenna 1, flagellum	Equal to or longer than peduncle	Shorter than peduncle
4.	Antenna 2, dimorphism	Not (or slightly) sexually dimorphic	Distinctly sexually dimorphic in form
5.	Antenna 2, peduncle	Not (or slightly) thickened (incrassate)	Distinctly incrassate in ♂
6.	Antenna 2, peduncular segment 4	Slightly shorter than peduncle 5 (especially in ♀)	Much shorter than peduncle 5 (in ♀)
7.	Mandible, left lacinia	More or less 5-dentate	4-detate; *6-dentate*
8.	Maxilliped palp	Short, broad	Tall, segment 3 subconical
9.	Maxilliped palp, segment 4	Present; distinct or masked by spines of 3	Fused variously to 3 or totally lacking
10.	Maxilliped palp, segment 2	Lacking mediodistal lobe	With mediodistal lobe
11.	Coxa 1	Rounded anterodistally	Acute or subacute anterodistally
12.	Coxa 5, anterior lobe	Shallow, distinctly less than coxa 4	Deep, subequal to depth of coxa 4
13.	Coxa 6, posterior lobe	Shallow, longer than deep	Deeper than long
14.	Coxa 6, posterior lobe, anterior margin	Rounded distally	Right-angled or with anterodistal process
15.	Gnathopod 1 (♂) subchelation	Strong, dactyl not exceeding palm	Weak, dactyl exceeding palm; *simple, palm lacking*
16.	Gnathopod 1 (♂), segment 4	Posterior tumescent lobe present, occasionally very small	Tumescent lobe totally lacking
17.	Gnathopod 1 (♂) Carpus (segment 5)	Short, posterior margin about half anterior margin	Elongate, posterior margin ¼ anterior margin
18.	Gnathopod 1 (♂) Propod (segment 6) length	Short (straight), length about twice maximum width	Elongate (arcuate), length 3–5 times maximum width
19.	Gnathopod 1 (♂) Propod tumescence	Postero-distal tumescent lobe large, distinct	Posterior lobe weak, flat, barely visible or lacking
20.	Gnathopod 1 (♀) subchelation	Strong, dactyl not (or very slightly) exceeding palm	Weak, dactyl exceeding palm
21.	Gnathopod 1 (♀) propod palm	Present, distinct	Lacking, or trace only
22.	Gnathopod 1 (♀) Propod tumescence	Postero-distal tumescent lobe present (may be vestigial)	Postero-distal tumescent lobe totally lacking
23.	Gnathopod 2 (♂), subchelation	Strongly subchelate, amplexing form	Neotenically arrested at transforming stage; *mitten-like (as in ♀)*
24.	Gnathopod 2 (♂), propod palm	Smoothly convex	Toothed, incised; *Sinuous, concave*
25.	Gnathopod 2 (♂), dactyl	Regular, smoothly arcuate	Toothed behind; *sinuous*

*Note: Second, or alternate apomorphic state is italicized.

Table 1 Cont'd.

No.	Taxonomic Character	Phyletic State	
		Plesiomorphic	Apomorphic
26.	Gnathopod 2 (♀), basis	Sublinear or slightly broadened anteriorly, margins subparallel	Distinctly broadened anteromedially, anterior margin arcuate
27.	Gnathopod 2 (♀), segment 4, posterior process	Broadly rounded	Long, acute; *lacking*
28.	Peraeopods 3 and 4	Similar in size and form	Peraeopod 4 distinctly shorter
29.	Peraeopod 4, segment 5	Normal, length 2–4 times maximum width	Very short, length about equal to width
30.	Peraeopods 3 and 4, dactyl form	Subequal in form and size	Dactyl 4, body pinched, shorter and stouter than dactyl 3
31.	Peraeopods 3–7	Simplidactylate; non-cuspidactylate (or cusps minute)	Cuspidactylate; cusps distinct, well developed
32.	Peraeopods 3 and 4, dactyl length	Short, length about twice width	Long, length 3–4 times maximum width
33.	Peraeopods 5–7, form	Homopodous; bases similar in form, or nearly so (♀)	Heteropodous; bases distinctly unlike in shape
34.	Peraeopod 5, form	Not unusually small, or differing (segments 3 & 4)	Very much smaller and of different form from peraeopods 6 and 7
35.	Peraeopod 5, dactyl	Normal, as in peraeopods 6 and 7	Very short, modified, stout, nail often vestigial
36.	Peraeopods 6 and 7, length	Peraeopod 7 longer	Peraeopod 6 longer
37.	Peraeopods 6 and 7, dimorphism	Not sexually dimorphic in form	Sexually dimorphic in form (especially peraeopod 7)
38.	Peraeopods 5–7, dactyls	Short, length 2–3 times maximum width	Elongate, slender, length more than 3 times width
39.	Pleopods	Subsimilar; all of normal length	Unequal in size; one or more reduced
40.	Pleopod rami	Normal, not (or little) shorter than peduncle	One or more pleopods with rami distinctly shorter than peduncle
41.	Pleopod peduncles, form	Linear or sublinear	Broadened or expanded laterally and/or basally
42.	Pleopod peduncles, armature	Outer margin smooth or nearly so	All peduncular outer margins spinose throughout
43.	Uropod 1, prepeduncle	Short, depth greater than length	Elongate, length greater than depth
44.	Uropod 1, armature	Weakly spinose; spines few and/or short	Strongly spinose; spines numerous (6–10 per segment) and/or long
45.	Uropod 1, peduncle	Disto-lateral (inter-ramal) spine well developed	Disto-lateral spine very small or lacking
46.	Uropod 1, outer ramus	Margin lacking spines (or nearly so)	Marginally spinose (3–many)
47.	Uropod 2, rami	Subequal	Outer ramus distinctly the shorter
48.	Uropod 2, inner ramus	Marginal spines in single row	Marginal spines in 2 rows
49.	Uropod 2, apical spines	Normally slender, tapering tips acute	Some spines with spade-like tips (spade spines)

Table 1 Cont'd.

No.	Taxonomic Character	Phyletic State: Plesiomorphic	Phyletic State: Apomorphic
50.	Uropod 3, peduncle form	Not markedly expanded, length greater than depth	Strongly expanded behind, depth (width) about equal to length
51.	Uropod 3, ramus length	Shorter than peduncle	Equal to or much longer than peduncle; *extremely short* (length = width)
52.	Uropod 3, ramus form	Cylindrical, tapering	Laterally compressed, margins subparallel
53.	Uropod 3, ramus apical spines	One or more spines stout, elongate	All spines weak, short
54.	Telson, form	Elongate, spade-shaped	Short, broad, length not greater than width
55.	Telson, apex	Variously cleft, lobes distally separated	Lobes distally fused to single plate
56.	Telson, armature	Apical and/or lateral spines only	Dorsal, plus apical and lateral spines
57.	Brood plates, size and form	Large, broadly subovate	Small to medium, narrowly ovate or sublinear
58.	Brood plate, peraeopod 5	Large, only slightly smaller than 2–4	Much smaller than 2–4 (except when 2–4 lacking)
59.	Brood plates, marginal setae	Tips hooked or clavate	Tips simple, tapering
60.	Coxal gills, form	All plate-like, or sac-like, little differing in size, little modified	Peraeopods 3–5 (especially) reduced, acetabulate, or very small; *enlarged, convoluted, and/or elongate*

Table II. Non Substrate Modifiers and Character States Considered

Character No.	Eye 2	A_1 4	Md 7	Mxpd 8	Mxpd 10	G_1 ♂ 16	G_1 ♀ 20	G_1 ♀ 22	G_2 ♂ 24	G_2 ♂ 25	G_2 ♀ 26	G_2 ♀ 27	P 3 & 4 28	P 3 & 4 30	Dactyls 31	P 5–7 33	P7 37	P 6–7 38	Pleopods 40	Pleopods 42	U_1 45	U_1 46	U_2 48	U_3 50	U_3 51	T 54	T 56	Br. plate 57	Br. set. 59	Gills 60	Apomorphy Tot/30
A. *Protorchestia*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B. *Pacificorchestia klawei*	0	0	0	0	1	0	0	0	0	0	0(-)	0	1(-)	1	0	0	0(+)	0	1(-)	0	0	1	0	1	0(+)	0	0	0(+)	1	0	7
C. *P. tenuimana*	0	0	0	0	1(-)	0	0	0	0	0	1(-)	0	1(-)	0+	1	0(+)	0	0(+)	1	0	0	0	0	1	0	0	0	0(+)	1	0(+)	7
D. *P. pyatakovi*	0	0	0	0	1	0	0	0	0	0+	1(-)	0	1(-)	0+	1	0(+)	0	0(+)	1	0	0	0	0	1	0	0	0	0(+)	1	0	7
E. "O". *vaggala*	1	0	1	1	0+	0	1	1	1	1	0	0	0	0(+)	0(+)	1	0	1	0+	0	0	0	0	0	/	0	0(+)	1	1	0(+)	8
F. "O". *costaricana*	0	0	1	1	0+	0	1	1	1	1	0	0	0	0(+)	0(+)	1	0	1	0+	0	0	0	0	0	/	0	0	1	1	0(+)	12
G. *Arcitalitrus*	0	0	1	0	0	1	1	1	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	/	0	0	1	1	0	11
H. *Talitroides*	0	0	1	1	0	1	1	1	0	0	0	0	1	0	1	1	0	1	1	0	0	0	0	0	/	1	0	1	1	/	12
I. *Transorchestia*	0	1	1	0	1	0	0	1	(1)	(1)	1(-)	0	1	1	1	1(-)	1	0	0	0	0	0	0	0	/	1	0	1	1	/	15
J. *Traskorchestia traskiana*	1	0	0(+)	1	1	0	1(-)	1	0	0	1(-)	0	1	1	1	0	0	0	0	1(-)	1	1	1(-)	1(-)	0	0	0	0	0	0(+)	17
K. *T. georgiana*	1	0	0(+)	1	1	1	1	1	0	0	1(-)	0	1	1	1	0(+)	0	0	1	0(+)	1	1	1	1(-)	0	1	1	0	0	1	16
L. *T. ochotensis*	0	0	0(+)	1	1	1	1	1	0	0	1(-)	0(+)	1	1	1	1(-)	1(-)	0(+)	1	0(+)	1	1	1	1(-)	0	1	1	0	0	1	18
M. *T. dimari*	1	0	0(+)	1	1	1	1	1	0	0	1(-)	0(+)	1	1	1	1	1(-)	0(+)	1	0(+)	1	1	1	1(-)	0	1	1	0	0	1	19
N. *Platorchestia*	1	1	0	1	1	1	1	1	0	0	1(-)	0(+)	1	1	1	1	1	0(+)	1	0(+)	1	1	1	1(-)	0	1	1	0	0	1	20
O. "O." *fritzi*	1	1	0	1(-)	1	1(-)	1	1	1	1	1	0(+)	1	1	1	1(-)	1	1	0(+)	1(-)	1	(0)	(1)	0	0	1	1	1(-)	1	1	23
P. *Orchestia*	1(-)	(1)	1	(1)	1	1	1	1	(1)	(1)	1	/(-)	1	1	1	0(+)	1	1(-)	1(-)	0	(1)	(1)	1(-)	0	0	0	1	1	1	1	24
																										1	1	1	1	1	26

0 = plesiomorphic
1 = apomorphic
1(-) = weakly apomorphic
0+ = trending to apomorphic
( ) = most members of group in this state
/ = alternate apomorphic state

Table III. Substrate Modifiers and Character States Considered

Character No.	Eye 1	A_1 2	A_2 4	A_2 5	Md 7	Coxa 5 12	Coxa 6 13	G_1 ♂ 15	G_1 ♂ 18	G_1 ♂ 19	G_1 ♀ 21	G_2 ♂ 24	G_2 ♂ 25	G_2 ♀ 26	G_2 ♀ 27	P4 29	P5 34	P5 35	P6 >7 36	Pleopods 40	Pleopods 42	U_1 43	U_1 46	U_2 47	U_2 49	U_1 51	U_1 52	T 55	T 56	Brood plate 5 58	Apomorphy Tot/30
A. *Talorchestia*	(1)	0+	1	(0)	(0)	1	0	0	0	0	1	1-	0	1	0+	0+	0	0	0+	0	0	0+	(0)	0	0+	0+	1(-)	0	1	1	9
B. *Platorchestia*	0	1	1	(1)	0	0	1	0	0	0	0	1-	0	1	0	1	0	0	0	0	0	0	(0)	0	0	0	0	0	1	1	9
C. *Trinorchestia*	1	0	1	0	0+	1	0	1-	0	0	0+	0+	1	1-	1	0	0	0	1	0	0	0	1	0	0	1	1	1	1	1	14
D. *Talitrus*	0	0	1	0	0	1	1	1	1	1	1	/	/	0+	0	0	0	0	1(-)	0	0	0	1	1	0	0	0	1	0	0	13
E. *Orchestoidea*	1-	0	1	0	1	1	1	1	1	1	1	1	1	0	0	0+	0	0	1	1	1	0	1	0	0	0	1	1	0	0	17
F. *Pseudorchestoidea brito*	1	0	1	0	1	1	0	1	0	0	1	0+	1	1	1	0	1	1	0	0	0	0+	1-	0	1	0	0	1	1	1	16
G. *P. gracilis*	1	1-	0	0	1	1	0	1	0	0	1	1	1	1	1	0	1	1	0	0	0	1	1-	0	1	1	1	0	1-	1	19
H. *P. meridionalis*	1	1-	0	0	1	1	0	1	0	0	1	1	1	1	1	0	1	1	0	1	0	1	0	0	1	1	1	0	1-	1	19
I. *P. mexicana*	1	1	0	0	1	1	0	1	0	0	1	1-	1	1	1	0	1	1	0	1	0	0	1	0	0	1	1	1	0+	1	19
J. *P. biolleyi*	1	0	0	0	1	1	0	1	0	1	1	1	1	1-	1	0	1	1	0	0	0	1	0	1	1-	0+	1	1-	1-	1	19
K. *Megalorchestia californiana*	1	1	1	0	/	1	1-	1	1	0+	1	1-	0	1	1	0	0	0	1	1	1	0	1	0	0	1	1	1-	1	0	20
L. *M. pugettensis*	0	1	1	1	/	1	0+	1	1	0+	1	1	0	1	1-	1	0	0	1	1	1	0	1	0	0	1-	1	1	1-	1	21
M. *M. corniculata*	0	1	1	1	/	1	1	1	1	1-	1	1	0	1	1	1	0	0	1	1	1	0	1	0	0	1	1-	1-	1	1	23
N. *M. benedicti*	0	1	1	1	/-	1	0	1	1	0+	1	1	0	1-	1	1	0+	0	1-	1	1	0	1	1	0	1	1	1	1	1	22
O. *M. columbiana*	1	1-	1	0	/	1	0	1	1	1-	1	1	1	1	1	1	0	1	1	1	0	1	1	0	1	0+	1-	1	1	1	24
P. *M. minor*	1	1-	1-	0	/	1	0	1	1	1-	1	0+	1	1	1	0	1	0+	1	1	1	0	1	1	0	0+	1	1-	1	1	22
Q. *M. dexterae*	1	1	1	0	/	1	0	1	1	1	1	1	1	1	1	0+	1	1-	1	1	1	0+	1-	1	0	0+	1	1	1	1	24

0 = plesiomorphic
0+ trending to apomorphic
1 = apomorphic
1- = weakly apomorphic
( ) = most members of group in this state
/ = alternate apomorphic state

Table IV. All Talitridae; Character States

Character No.	1 Eye	2 A_1	4 A_2	7 Md	8 Mxpd	9 Mxpd	10 Mxpd	11 Coxa 1	15 G_1 ♂	16 G_1 ♂	17 G_1 carpus	18 G_1 propod	20 G_1 ♀	24 G_2 ♂	25 G_2 ♂	26 G_2 ♀	27 G_2 ♀	28 P3 and 4	30 P4 dactyl	31 P3–7 dactyls	33 P5–7	34 P5	36 P6 > 7	37 P7	40 Pleopods	41 Pleopods	42 Pleopods	43 U_1	45 U_1	46 U_1	47 U_2	48 U_2	50 U_3	52 U_3	55 T	56 T	58 Br. plate 5	59 Br. setae	60 Gills	90 Apomorphy
A. *Proterchestia*	0+	0+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B. *Pacifiorchestia*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7
C. "*O*" *wiggsi*	0	0	–	–	0	–	–	0	0	0	0	0	0	0	–	0	0	0	0	0	–	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10
D. "*O*" *consericana*	0+	0	0	–	0+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10
E. *Arcitalitrus*	0	0	0	–	0	–	0	0	–	–	0	0	0	–	–	0	0	0	0	0	–	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14
F. *Talitroides*	0	0	0	–	0	–	0	0	–	–	0	0	0	–	–	0	0	0	0	0	–	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14
G. *Transorchestia*	0	0+	0	–	0+	–	0+	0	0+	0+	0	0	0	0	0	0	0	0	0	0	–	0+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17
H. *Traskorchestia*	0	(1)	0	0+	0+	–	–	0	0	(1)	0	0	0	0	0	0	0	0	0	0	–	0+	0	0	(0)	0+	0+	0+	0	0	0	0	0	0	0	0	0	0	0+	15
I. *Platorchestia*	0	–	–	0	–	–	–	0	0	0	0	0	0	0	0	0	0	0	0	0	–	0	0	0	(1)	(0)	0+	0	0	0	0	0	0	0	0	0	0	0	–	16
J. *Orchestia*	0	–	–	0	–	–	–	0	0	0	0	0	0	0	0	0	0	0	0	0	–	0	0	0	(1)	(0)	0+	0	0	0	0	0	0	0	0	0	0	0	–	19
K. *Talorchestia*	(1)	(1)	–	0	0+	–	0+	0	0+	0+	0+	0	0	(1)	(1)	0+	0+	0	0	0	–	0	0	0	(1)	(0)	0	0	0	0	0	0	0	0	0	0	0	0	–	22
L. *Talitrus*	0	–	–	0	–	–	–	0	0	0	0	0	0	(1)	(1)	0	0	0	0	0	–	0	0	0	(0)	0	0	0	0	0	0	0	0	0	0	0	0	0	–	26
M. *Orchestoidea*	1–	–	–	–	–	–	–	0	0	0	0	0	0	/	/	0+	/	0	0	0	–	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	25
N. *Trinorchestia*	1	–	–	–	–	–	–	0	0	0	0	0	0	/	/	0+	/	0	0	0	–	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0+	1–	31
O. *Pseudorchestoidea*	1	–	–	0	–	–	–	0	0	0	0	0	0	/	/	/	/	0	0	0	–	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	28
P. *Megalorchestia*	1	–	0	1–	–	–	–	0	0	0	0	0	0	/	1–	/	/	0	0	0	–	0	0	0	0	0	0	0	0	(0)	(0)	(0)	0	(0)	0	0	0	0	–	28
	(1)	–	–	/	–	–	–	0	0	0	0	0	0	0	1–	0	0	0	0	0	–	0+	0	1	0+	1	1	0	–	1	1	–	0	1	1	(1)	–	–	–	35

0 = plesiomorphic
0+ = trending to apomorphic
1 = apomorphic
1– = weakly apomorphic
( ) = most members of group in this state
/ = alternate apomorphic state

Table V. Distribution of North Pacific Beach Fleas and Landhoppers

TAXONOMIC UNIT 1. Talitridae Beach Fleas and Landhoppers	S. Japan, China Sea	North Japan Sea	Okhotsk, Sakhalin, Hokkaido	Western Pacific, Kamchatka	Aleutians	Prince William Sound	Cross Sd. to Dixon & Q.C.I.	N. B.C. to N. V.I.	Central B.C. to S. V.I.	Washington	Oregon & North California	California South Conception	Cortez	Mexican Province	Panamic Province
1. *Paciforchestia*															
tenuimana (Iwasa)	X	X													
pyatakova (Derzh.)	X	X													
klawei (Bousf.)									X	X	X	X			
kokuboi (Ueno)	X	X													
2. *Traskorchestia*															
dzimari (Derzh.)			X												
ochotensis (Brandt)			X	X	X	X									
traskiana (Stimps.)					?	X	X	X	X	X	X	X			
georgiana (Bousf.)								X	X	X	X	X			
3. *Transorchestia*															
enigmatica (B. & C.)											•				
3. *Platorchestia*															
platensis (Kr.)	X	X													
crassicorne (Derzh.)															
japonica (Tatsen.)	X	X													
zachsi (Derzh.)															
chathamensis n.sp.									X	?					
4. "O." *solifuga* I. n.sp.	X	?													X
5. *Orchestia*															
cuticriana Sieb.															X
6. *Arcitalitrus*															
sylvaticus (Haow.)											•				
7. *Talitroides*															
topitotum Burt												•			
Total	6	5	2	1	1	2	1	2	4	3	5	4	0		2
Total talitrids	9	9	6	2	2	4	3	4	7	6	10	9	1		5

Table VI. Distribution of North Pacific Talitroidean Amphipoda: Sandhoppers

TAXONOMIC UNIT 1. Talitridae Sandhoppers	S. Japan, China Sea	North Japan Sea	Okhotsk, Sakhalin, Hokkaido	Western Pacific, Kamchatka	Aleutians	Prince William Sound	Cross Sd to Dixon & QCI	N BC to N VI	Central BC to S VI	Washington	Oregon & North California	California South of Pt. Conception	Center	Mexican Province	Panama, Peninsular
1. Talorchestia															
nipponensis Morino	x	x													
siamia Tattersall	x	x	x												
julicipes ?	x	x?													
2. Traskorchestia															
traskiana (Derzh.)		x	x	x											
3. Pseudorchestia															
crassicornis (Derzh.)		x	x	?	?										
zacha (Derzh.)			x												
frizzi (Muller)			x												
4. Megalorchestia Bdt															x
pugettensis (Dana)					x	x	x	x	x	x	x				
corniculata (Stout)											x	x			
benedicti (Shoem)											x	x			
californiana Brit											x	x			
columbiana (Bousf)					?	x	x	x	x	x	x	x			
minor (Bousf.)											x	x			
dexterae (Bousf.)												x	x		
5. Pseudorchestoides															
gracilis (B&K)													x	?	
mexicana n.sp.														x	
neridomaris (Schout.)															x
hulleyi (Stebb.)															x
Totals	3	4	4	1	1	2	2	2	3	3	5	5	1	1	3